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Contents

Distribution and habitat of the land snail *Tasmaphena lamproides* (Pulmonata: Rhytididae) in Tasmania

Kevin Bonham

Flat 3 54 Duke Street, Sandy Bay, Tasmania 7005

and

Robert J. Taylor

Forestry Tasmania
GPO Box 207B, Hobart Tasmania 7001
email: Rob.Taylor@forestry.tas.gov.au

The carnivorous snail *Tasmaphena lamproides,* believed to be endemic to northwest Tasmania and far southern Victoria, has been considered rare. A survey in the Togari forest block in northwest Tasmania suggests that the species occurs in a wide range of forest habitats but requires deep leaf litter to survive, and is more frequent in the north of the block. Knowledge gained from this survey, combined with known records, suggests a range of at least 25,000 hectares and an improved outlook for the species.

Introduction

Tasmaphena lamproides (Cox, 1868) (Gastropoda: Pulmonata: Rhytididae) is a large carnivorous land snail considered to be rare. Carnivorous snails are generally less numerous than snails at lower trophic levels. However, *T. lamproides* also appears to have a restricted distribution. Smith and Kershaw (1981) recorded it from only five 10 km grid squares in northwest Tasmania.

In this paper we collate the distribution records for *T. lamproides* and report on the habitat requirements of the species revealed from a detailed survey of part of its range.

Previous Distribution Records

Tasmaphena lamproides was discovered by Cox in the late 1860s and described (as *Helix lamproides*) by him in 1868. Petterd (1879) suggests that Circular Head was the type locality. There were a number of collections of the species during the 1870s, but it is difficult to determine by whom these were made, since most appear only in monographs. Petterd listed the localities of Table Cape, Circular Head and Duck River, with a note that the North West Bay locality given by Legrand in 1871 was almost certainly an error resulting from mis-labelling.

The Table Cape record is apparently due to Petterd. He notes that it occurred under logs in "dense fern-tree scrubs" at the Duck River (probably at Smithton or slightly further south) but at a drier locality at Circular Head. However, he gives no detail of the habitat at the Table Cape site, nor does any other author, and there has been no other record within 30 km of Table Cape. Furthermore, Ron Kershaw (pers. comm.) notes that records given by Petterd are sometimes unclear due to insufficient or confused labelling. Under these circumstances the record is highly dubious.

Petterd and Hedley (1909) state that *T. lamproides* "is strictly confined to the north-western scrubs where it is not uncommon" and also recorded some very large specimens from Montagu River. Specimens which have since been found near the southern parts of the Montagu River are far smaller
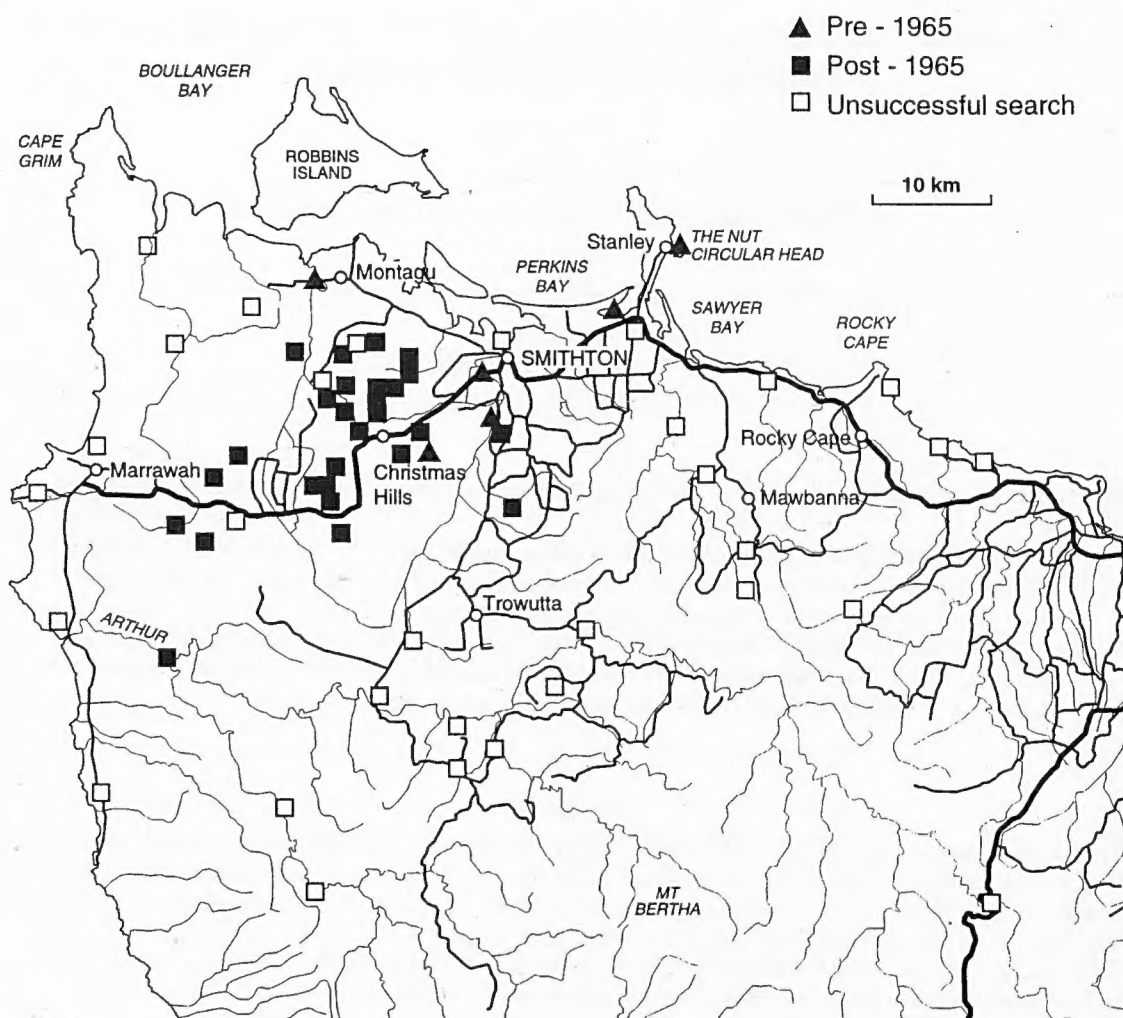
Figure 1.   Distribution records for *T. lamproides* and searches undertaken for the species which have been unsuccessful. The old record from Table Cape is considered dubious (see text) and has not been included.

than the suggested size of 29 mm (shell width). This suggests that the large specimens may have come from the northern end of the river.

Kershaw (pers. comm.) suggests the record from Circular Head may have been inland (e.g. Christmas Hills). This would not be surprising as early locality data were frequently imprecise. However, the past existence of the species near The Nut is confirmed by a specimen collected by B.C. Mollison at West Inlet in 1963 and held in the collections of the Tasmanian Museum, Hobart. This specimen is a whitened dead shell which may have been preserved by sand for some decades prior to collection. As it was found under a stone, the chance of it being accidentally brought to the area is remote. Thus it seems that *T. lamproides* was present there at some time in the past. The habitat now appears unsuitable and attempts to find it around The Nut since have failed.

Kershaw (pers. comm.) recorded the species from Christmas Hills "on hillside above the swamp in wet forest litter" in 1957. He indicates that he found it very difficult to find in the northwest and did not find many specimens.

During December 1988 and September 1991 live *T. lamproides* were recorded by K.B. at Turk's Landing (Arthur/Frankland Rivers, AMG 3128 54503, 25/12/88), Eldridge Road (3266 54619, 25/12/88) and near Jones Plain (3343 54708, 4/10/91). At all these sites the species was very difficult to find.

Bob Mesibov (pers. comm.) has found the species a number of times in recent years. Several of these records are from the northern part of the Togari forest block. Other records are from the Christmas Hills/Jones Plain area (3341 54702, 26/8/92), and from two different areas of Welcome Swamp (3146 54630, 9/7/92) (3169 54620, 25/9/92).

A number of apparently suitable areas in the northwest do not appear to support *T. lamproides*. It has not been found at Balfour, and attempts by K.B. to find it in the Sumac Loop area have yielded none in over 12 hours searching. Many areas around Black River and Rocky Cape have been searched unsuccessfully by various collectors. Distribution maps for other species in Smith and Kershaw (1981) indicate that some localities in the extreme northwest (Woolnorth–Mt Cameron–Montagu area) have been searched without success. *Tasmaphena lamproides* has also not been found on King Island despite some collecting effort.

T. lamproides also occurs on Wilson's Promontory, Victoria. S. A. Clark (pers. comm.) of the Australian Museum (Sydney) found it fairly easily on four separate visits. Clark confirms that Victorian and Tasmanian specimens are very similar. Some other Victorian records are rumoured but are unconfirmed by specimens. The distribution across Bass Strait is slightly unusual as several commoner medium to large Tasmanian snails are endemic.

Methods

An intensive survey of *T. lamproides* was undertaken in the Togari Forest block, an area of around 8600 ha northwest of Christmas Hills in northwest Tasmania (Fig. 2). Elevation varies between 30–100 m and Togari mudstone (yellow clay) soils predominate. Most of the area is dominated by *Eucalyptus obliqua* with Blackwood (*Acacia melanoxylon*) dominating in the gullies. The area was cut-over in the 1950s and 60s and so the old growth present is mixed with regrowth of differing densities depending on the extent of past disturbance. This old growth covers about 25% of the area, with non-eucalypts, including Blackwood, covering 15%, with the rest being mainly regrowth eucalypt. The undergrowth is dominated by the shrubs *Pomaderris apetala*, *Acacia mucronata*, *Zieria arborescens*, *Oleria argophylla*, *Leptospermum* spp., *Melaleuca* spp., the tree fern *Dicksonia antarctica* and the sedges *Gahnia grandis* and *Lepidosperma elatius*. The rainforest trees *Nothofagus cunninghamii* and *Atherosperma moschatum* also occur on some sites.

Fieldwork was conducted between 7–11 and 14–17 September 1992. Twenty-nine plots were surveyed (by Kevin Bonham and Michael Mahoney). Each plot was a circle of radius 15 m. A larger sampling area would have involved greater searching time at each site and would have prevented a sufficient range of sites from being covered, while smaller plots would not have yielded sufficient numbers of *T. lamproides* to enable meaningful comparisons between sites and would have led to excessive time wastage in travelling between sites. Twenty-nine sites were selected so as to sample the range of vegetation types and spread plots across the block. Time taken to search a plot and identify specimens varied from 70 to 120 minutes according to the amount of suitable shelter present, which was greatest on gently sloping sites and sites with a large number of small trees. Identification of *T. lamproides* was straight forward except for one specimen which caused some confusion because it lacked the lateral keel present strongly in all other known individuals. Specimens of *T. lamproides* were classed as alive or dead and as adult or juvenile. Specimens were classified as "adult" if shell width was 14 mm or greater. Full size is around 21 mm. In the absence of any anatomical work on the species this was thought to provide a better estimate than whorl count.

Site details recorded included grid reference, age of forest (whether regrowth or old growth, and estimated age if the former), dominant plant species present, degree and direction of slope. Forest age was estimated in the field and checked against forest age maps held by Forestry Tasmania. Every

LIKELY HABITAT

POSSIBLE HABITAT

10 km
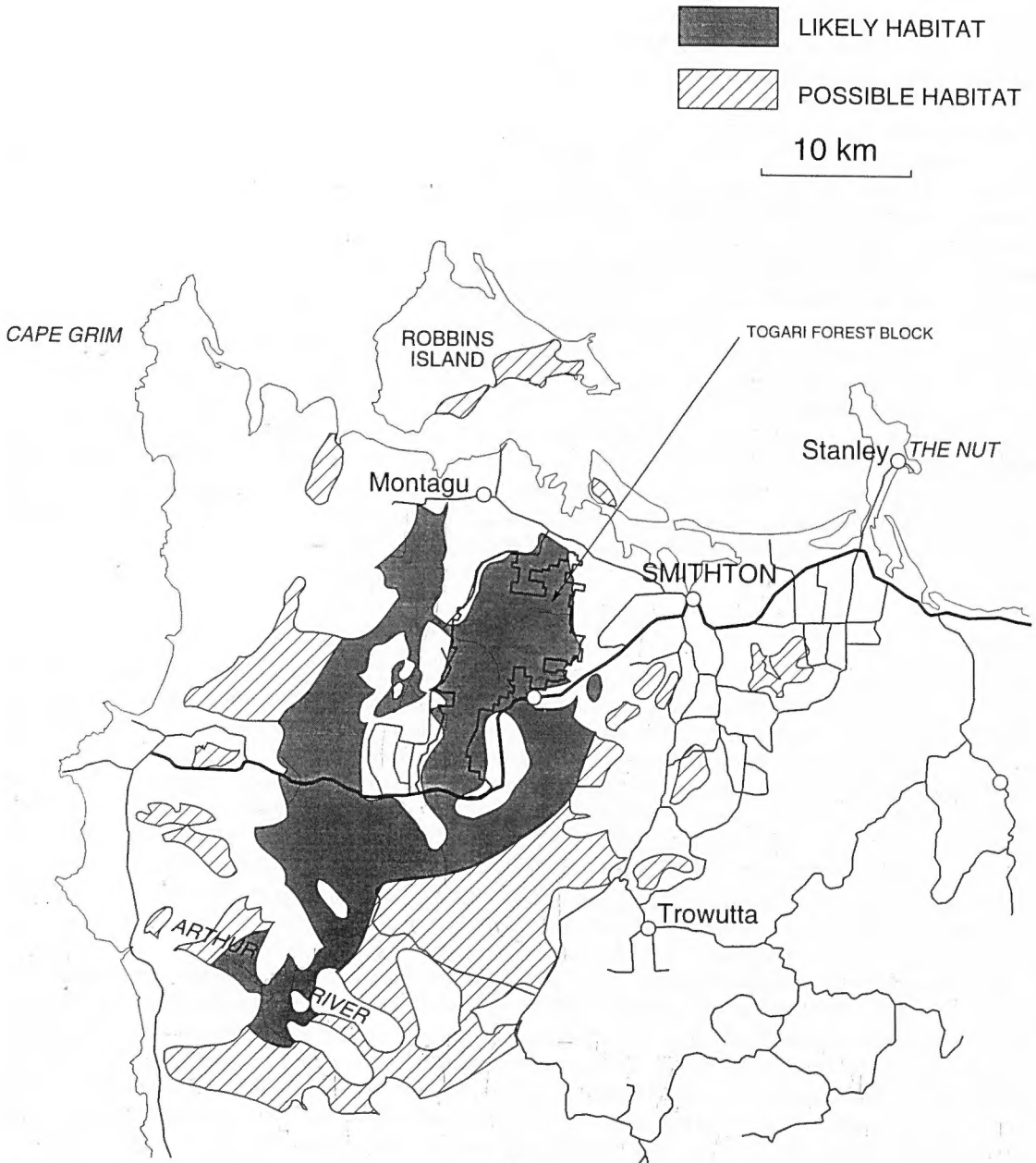
Figure 2.   Extent of the occurrence of habitat that is likely to contain, or may possibly contain, *T. lamproides*. The intensive study area (Togari forest block) to the west of Smithton is outlined in black.

attempt was made to ensure undergrowth conditions were representative of the area selected, but at some sites this was difficult to do.

All available shelter was searched, including the undersides of logs and stones, piles of sufficiently deep leaf litter (especially around the bases of trees), and the insides of logs sufficiently decomposed to be broken apart. It is likely that some specimens were missed, particularly those sheltering under logs too large to move. However, of the many logs that required any persistent effort to move, only

one had a *T. lamproides* under it and the specimen was not far away from the edge of the area covered by the log. *T. lamproides* is not known to climb trees.

Other mollusc species encountered were also counted and numbers of potential prey species and predatory species (which may compete with *T. lamproides*) were correlated with numbers of *T. lamproides*. Both total numbers and numbers of live *T. lamproides* were used in the analysis. Numbers of live adults can be prone to weather-related variations in crypticity and to small sample size when used alone. Numbers of dead adults may represent relics of past populations under different ecological conditions, while juvenile numbers may be unsuitable due to variation in juvenile mortality.

Correlations were determined using either Pearsons or Spearman rank correlation coefficients. Stepwise multiple regression was used to investigate linear relationships between a variable and several others. Two means were compared with t-tests.

Results

Distribution

Sites where *T. lamproides* has been recorded, including those from the present study and subsequent records, are shown in Fig. 1. In many cases, particularly older records, the locality shown is only approximate. Successful searches very close to each other have been shown as one record, while some unsuccessful searches very close to successful ones have also been omitted. The unsuccessful searches shown are certainly not all that have occurred in the area shown, but are included to give some indication of likely restrictions upon the range of the species. The area around Mt Bertha has been extremely poorly searched but the large number of recorded non-occurrences north, west and northwest of that area suggest it is unlikely that *T. lamproides* occurs there.

An assessment of the likely range of *T. lamproides* is provided in Fig. 2. The species has been considered likely to occur in areas of suitable habitat close to and continuous with recent records. Areas of suitable habitat where the evidence is unclear are also indicated. For instance there has been no searching in the scrub areas on Robbins Island. The biggest areas of uncertainty are around the southern end of the Montagu River, where over 100 km2 of suitable habitat has never been searched. The record from the Arthur/Frankland junction suggests the species may occur this far south. Around 25,000 hectares of habitat are considered likely to contain *T. lamproides*, with at least another 20,000 hectares unclear. About 7,000 hectares west of the northern part of the Togari block probably contains good populations of *T lamproides* but is owned by North Forest Products and future land use here is uncertain. A few small areas are privately owned but these are not likely to be of great significance. The remaining likely range of the species is largely within State forest.

Habitat Use

A total of 17 native and two introduced molluscs were recorded from the sampled plots in the Togari forest block. Numbers (including live and dead specimens) of each species (listed according to family) are as follows:

RHYTIDIDAE: *Victaphanta milligani* 174, *Tasmaphena lamproides* 82, *Prolesophanta dyeri* 8, *Prolesophanta nelsonensis* 2.

CHAROPIDAE: *Pernagera kingstonensis* 5, *Allocharopa legrandi* 15, *Discocharopa mimosa* 1, *Roblinella gadensis* 1, *Oreomava johnstoni* 6, *Bischoffena bischoffensis* 1, *Thryasona diemenensis* 6, *Stenacapha hamiltoni* 485.

PUNCTIDAE: *Paralaoma caputspinulae* 1, *Pedicamista* sp. 2, *Trocholaoma parvissima* 1.

CYSTOPELTIDAE: *Cystopelta bicolor* 5.

HELICARIONIDAE: *Helicarion cuvieri* 142.

LIMACIDAE: *Deroceras reticulatum* (Introduced) 1.

ARIONIADE: *Arion intermedius* (Introduced) 3.

Some species, especially *Cystopelta bicolor*, occur in different microhabitats to that of *T. lamproides*, and thus the numbers recorded are not a true indication of the relative frequencies of the species. The semi-slug *Helicarion* (a dietary item of *T. lamproides*) appears to be quite common but only 3 of the 142 seen were alive.

T. lamproides did not occur at any site in particularly great numbers. The maximum recorded at a site was ten, four of which were live specimens. A large carnivorous snail has considerable demands for food and thus cannot occur in very large numbers unless food is abundant. However, *T. lamproides* is clearly one of the more numerically significant species in the block. Only two other species, namely *V. milligani* and *S. hamiltoni*, were more often found alive. Eighty-two (8.75%) of 937 native molluscs found were *T. lamproides*, and on sites potentially suitable for it, it averaged 11.3% of all snails found. Although this figure is inflated by the fact that searching effort was concentrated on this species, it still compares very favourably with the equivalent figures for related species, such as *T. sinclairi* which accounts for a mean 7% in the habitats in other areas where it is present (K. Bonham, unpubl. data). The evidence thus suggests that *T. lamproides* is no rarer than one would expect of a large carnivorous snail in such habitat.

Tasmaphena lamproides occurred at 23 of the 29 sites surveyed. Of 82 specimens found there were 20 live adults and 11 live juveniles, 31 dead adults and 20 dead juveniles. The majority of specimens were found associated with logs or accumulations of litter (Table 1). Most dead specimens were found under logs or in other microhabitats which suggested they had lived in the area, and only a small number were particularly worn or decomposed. Two sites had large numbers (five and six) of dead shells only. Live specimens occurred at 15 sites. The number of dead shells at a site was not correlated with the number of live animals found but the number of live adults was correlated with the number of live juveniles ($r_s = 0.48$, $p<0.05$).

At the two sites where only a single dead shell was found it is likely that these shells had been transported to the sites by a bird or mammal as both were badly damaged in a manner consistent with predation and they were not under logs or stones. *T. lamproides* was considered absent from these sites in subsequent analyses.

Sites where invertebrates populations appeared to be low were generally poor sites for *T. lamproides*. The range of invertebrates included in the diet of *T. lamproides* is not known. During

Table 1.   Occurrence of *Tasmaphena lamproides* in different microhabitats from sites surveyed in the Togari Forest Block west of Smithton in northwest Tasmania.

Microhabitat	Live Adult	Live Juvenile	Dead Adult	Dead Juvenile	TOTAL
Under logs	6	1	12	3	22
In rotten logs	1	–	–	–	1
Litter around logs	2	1	2	4	9
Litter at base of *Dicksonia* fern	5	1	1	–	7
Litter at base of *Pomaderris*	4	3	5	1	13
Litter at base of *Olearia*	–	3	–	1	4
Litter at base of blackwood	–	–	–	1	1
Litter at base of eucalypt	–	–	1	1	2
Litter in ditches and depressions	2	1	7*	3	13*
Litter in the open	–	1	1	6	8
On open ground	–	–	2*	–	2*

* Includes one badly damaged shell possibly transported to the site by animals.

the survey, two live adult *T. lamproides* were observed feeding on *S. hamiltoni*, a very common charopid snail. The only other non-predatory snail species present which occurred in reasonable numbers and was greater than 3 mm in size was *H. cuvieri*. Several dead *H. cuvieri* specimens were in a crumpled condition consistent with predation by *Tasmaphena*. Combined numbers of *S. hamiltoni* and *H. cuvieri* were used as an index of snails potentially available as prey. Total numbers of *T. lamproides* ($r = 0.51$, $p<0.01$), but not numbers of live individuals, were significantly correlated with the combined numbers of *S. hamiltoni* and *H. cuvieri*. *T. lamproides* was absent from a site where a large number (39, including 23 alive, 16 of those adult) of *V. milligani* (another predatory species of mollusc) was found. The number of *V. milligani* was significantly negatively correlated with total numbers of *T. lamproides* ($r = -0.39$, $p<0.05$) but not with the number of live *T. lamproides*. A multiple regression of total numbers of *T. lamproides* (but not number of live *T. lamproides*) against numbers of predators and non-predatory snails was significant ($F(2,26)=8.6$, $p<0.01$; $r = 0.63$).

Total number of *T. lamproides* = 0.096 P - 0.093 Vm + 1.23 where P = numbers of prey (*S. hamiltoni* and *H. cuvieri*) and Vm = numbers of *V. milligani*.

The apparent lack of invertebrate prey and associated lack of *T. lamproides* populations often appeared to be associated with poor development of the litter layer. The litter layer is destroyed by hot regeneration burns undertaken after logging or by intense wildfires but builds up again as the regrowth forest ages. To examine the effects of forest age on *T. lamproides*, populations in young regrowth (<60 years) were compared with those in older forest (> 60 years). One of the mature forest sites was extremely swampy and it is likely that the ground would have been underwater for much of the year. The absence of the species here was probably not associated with lack of litter and this site was excluded from this analysis. Total numbers of *T. lamproides* in young regrowth sites (1.00±1.26 (X±SD))was significantly less ($t = 2.12$, df=26, $p<0.05$) than for older forest (3.36±2.56).

Populations densities (live and dead) of *T. lamproides* in older forest in the north of the Togari block (north of around the 76 grid line) (5.25±2.76, N=8) were significantly greater (t=3.21, df=21, $p<0.01$) than those in older forest in the southern section (2.13±1.88, N=15).

Discussion

The lack of any correlation between numbers of live animals and dead shells suggests that population numbers at a site may fluctuate dramatically. For example, there were exclusively numerous dead shells at two sites which showed no unusual preservation conditions. Population explosion and die-off has been observed in many Tasmanian snails including *V. milligani* (K. Bonham unpubl. data). With this in mind, we consider that total numbers more reliably indicate habitat quality.

The basic needs of *T. lamproides* would encompass adequate food supplies including calcium for shell growth, moisture, shelter from predators, and protection from adverse weather. *T. lamproides* was found to be absent from sites with poor litter development and/or invertebrate populations. This is probably related to a low abundance of food as suggested by the correlation between numbers of *T. lamproides* and numbers of nonpredatory snails. Little is known regarding the prey of *T. lamproides*, and thus comprehensive data on food availability could not be gathered to determine how the abundance of prey affected the species. The small number of shells found that had been damaged by vertebrates suggests a lower rate of predation from vertebrates than for some other large Tasmanian snails such as *Anoglypta*, *Caryodes* and *Bothriembryon*.

The absence of *T. lamproides* from one site was probably related to the swampy conditions and its absence from an extremely sandy site could have been related to a calcium deficiency in the soil or to the lack of shelter in the form of logs or litter accumulations. There was a significant negative correlation between numbers of *T. lamproides* and other predatory snails, and *T. lamproides* was absent from a site where the other major predatory species, *V. milligani*, was abundant. This suggests that competition plays a role in influencing population levels of *T. lamproides*. However, since the number of *V. milligani* was only significantly negatively correlated with total numbers of *T.*

lamproides and not with numbers of live individuals, it is possible that the significant correlation may be due to the destruction of dead shells by other predatory snails as a way of obtaining calcium. A specimen of *V. milligani* was observed eating a *T. lamproides* shell once during the survey. *Victaphanta milligani* is known to eat worms (B. Mesibov, pers. comm.) and can travel into the soil for some distance where a hole of some form already exists. It was frequently observed entering holes too small for an adult *T. lamproides* to fit into.

T. lamproides was absent from young silvicultural regrowth. This may be due to low levels of litter and associated low abundances of invertebrates in these forests (Madden *et al.* 1976, Neumann 1991). However, it appears that logging may not have a detrimental effect on the species in the long term. Older regrowth is just as supportive of the species as old growth. *T. lamproides* has thus been able to recolonise areas as they have aged. The age of the forest at which *T. lamproides* populations redevelop to their prelogging levels is not known precisely. From the regrowth examined in this study it appears to be greater than 30 years and less than 60 years. Population levels may be influenced by the build up of the litter layer and consequent increase in invertebrate numbers. Brown and Nelson (1992) state that at least 50 years is required before litter is consistently well-developed in wet forest regrowth after logging and burning in Victoria.

A pronounced concentration of *T. lamproides* was found in the northern sites. This finding is further supported by subsequent searches by M. Mahoney (pers. comm.) in the Redpa area, which is further south but classified as being similar to the forest in the north of the Togari block. This work did not produce numbers *of T. lamproides* equivalent to that of the northern sites in Togari. Searches undertaken by Bob Mesibov (pers. comm.) also suggest *T. lamproides* is more common in the north of the block. It is possible that this geographical anomaly is produced by more favourable climate in the northern areas, but there is no evidence for this. It does not appear to be controlled by slope as the most productive sites varied in their aspect. No conclusive explanation for the differences exists at present.

The constraints restricting *T. lamproides* to such a small range are not clear. To the east it may be out-competed by *T. sinclairi*. To the south it is possible that it becomes less common as areas become too cold for either it or some section of its diet to survive. Within its limited range it is apparently neither particularly rare nor abnormally sporadic, and it appears to be, if anything, more tolerant than most snail species. It should be regarded as a species with a naturally limited range but not otherwise rare.

Within the Togari block, *T. lamproides* was reliably present in small numbers over a wide range of available habitats. *T. lamproides* was surprisingly consistent in its presence, being located at 72% of the sites. This compares favourably with all bar one of the other snail species present in the block, and also compares favourably with similar species in other areas of Tasmania. For example, the success rate at finding *T. sinclairi* in suitable habitat over searches of similar or greater extent to the sites searched in the present study is only 62% (K. Bonham, unpubl. data) and *T. sinclairi* occurs much more widely than *T. lamproides*, its known range including about 60% of Tasmania. The consistency with which *T. lamproides* occurs in the Togari block suggests that it is a quite tolerant species and that its perceived rarity is due mainly to its limited distribution and cryptic nature. The only identifiable threat to the species comes from destruction of habitat through logging, fire or clearing. The majority of the range of the species occurs on State forest and hence forest cover is expected to be maintained on these areas in the long term, although the species would probably be locally eliminated by plantation development. Since it reinvades regenerating native forest over time, the status of the species in the future will be determined by the proportion and degree of interconnection of native forest present which is 50 or more years of age, particularly in the northern section of the Togari block.

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Note added in proof: In February 1997 *Tasmaphena lamproides* was located by K.B. in two small areas of wet eucalypt forest on Three Hummock Island in Bass Strait. The specimens found were slightly smaller and had a darker shell colour than Tasmanian mainland specimens. Searches for the species on King Island (December 1996), Hunter Island (January 1997) and Robbins Island (February 1997) were unsuccessful.

Large Trachycardiinae from the Indo-West Pacific: The group of *Vasticardium orbita* (Broderip & Sowerby, 1833) (Mollusca, Cardiidae)

Jacques Vidal

Attaché au Museum National d'Histoire Naturelle
Laboratoire de Biologie des Invertébrés
Marins et Malacologie
55 rue Buffon, 75005 Paris, France

Key words: Mollusca, Cardiidae, *Vasticardium orbita*, Indo-Pacific.

Abstract

Two closely related species of Trachycardiinae from the Indo-West Pacific belonging to the *Vasticardium orbita* complex are revised. Young specimens are very similar in shell morphology but adult shells differ in general shape and rib structure. Based on these ontogenetic changes, and also on rib count, which appears to be a stable character, two species are recognised: (1) *Vasticardium orbita* (Broderip & Sowerby, 1833), with a mainly Pacific distribution and four subspecies: *orbita, hawaiiensis, mendanaense,* and *philippinense* and (2) *Vasticardium luteomarginatum* (Voskuil and Onverwagt, 1991), with a primarily Indian Ocean distribution and three subspecies: *luteomarginatum, marerubrum,* and *insulare*, the last of which is herein described as new.

The two species are usually easy to separate, but some specimens are difficult to differentiate. The apparently allopatric distribution of the two species raises the possibility that a single species, with discrete geographical subspecies, is involved.

Introduction

Several Recent species of Indo-West Pacific Trachycardiinae regularly reach more than 80 mm in height, and sometimes can attain 140 mm. The 80 mm limit is reached by large specimens of very few other species in this subfamily, and most species do not reach this size.

The "large" species mentioned above form several groups: the group of *Vasticardium angulatum* (Lamarck, 1819) which has several forms but no defined subspecies (Vidal, 1991); the group of *Vasticardium elongatum* (Bruguière, 1789), with six described subspecies and numerous forms (Vidal, 1993); *Vasticardium fidele* (Vidal, 1992) is similar in shell morphology, but is a little smaller, the largest recorded specimen being only 75.3 mm in height; *Vasticardium papuanum* Vidal, 1996; *Vasticardium gortanii* (Nardini, 1937), a Red Sea fossil species (see below); and the *Vasticardium orbita* (Broderip & Sowerby, 1833) complex, which is examined here.

The present paper, together with the four cited above, concludes a revision of all the known living "large" *Vasticardium* from the Indo-West Pacific.

The most significant conclusion is that young individuals of different species or subspecies of the *V. orbita* complex are very similar in shape, sculpture and ornamentation of the ribs. These characters are different from those found in the other groups of large species of Trachycardiinae. As the shells of juvenile *V. orbita* grow, they are progressively modified so characters differ between juveniles and adults of the same species, as occurs in *V. elongatum* (Vidal, 1993). Using the nature and degree of these changes, and differences in other characters such as shape, colour or rib number, two species are recognised here: *V. orbita* from the Pacific Ocean with four subspecies: *orbita, hawaiiensis, mendanaense,* and *philippinense* and *V. luteomarginatum*, with a mainly Indian Ocean distribution and

three subspecies: *luteomarginatum*, *marerubrum*, and *insulare*, the last of which is herein described as new.

Details of the synonymy and shell morphology of both species and all of the subspecies are presented below. An alternative viewpoint, based largely on the allopatric distribution of the groups, is that there is a single, variable species. This problem is discussed at the end of the paper.

Materials and methods

Whereas *Vasticardium elongatum* and *V. angulatum* live in sheltered, shallow near shore environments, the available evidence is that *V. orbita* prefers a more exposed outer slope habitat. This explains why the species is relatively scarce in museum collections. Nevertheless, I have been able to examine about 300 specimens in 214 geographically widespread lots, including most of the type material. The ribs have been counted on almost all specimens, and shells of 200 individuals from 132 lots have been measured. The material comes from the following museums: AMS, Australian Museum, Sydney; ANSP, Academy of Natural Sciences, Philadelphia; BISHOP, Bernice P. Bishop Museum, Honolulu; BM(NH), The Natural History Museum, London; IRSNB, Institut Royal des Sciences Naturelles de Belgique, Brussels; LACM, Los Angeles County Museum, Los Angeles; MHNG, Museum d'Histoire Naturelle de Genève, Geneva; MNHN, Museum National d'Histoire Naturelle, Paris; NHMW, Naturhistorisches Museum, Vienna; NNM, Nationaal Natuurhistorisch Museum, Leiden; QM, Queensland Museum, Brisbane; UGML, University of Guam Marine Laboratory; UMZ, University Museum of Zoology, Cambridge; USNM, National Museum of Natural History, Smithsonian Institution; WAM, Western Australian Museum; ZMA, Zoologisch Museum, Amsterdam; ZMUC, Zoologisk Museum, Copenhagen.

In the subfamily Trachycardiinae numerous shells belonging to different species can have similar combinations of morphometric data (H = Height, L = Length, W = Width), hinge characters, colours, rib number, etc. On the other hand some of these characters, for example rib numbers, vary appreciably intraspecifically or with growth in an individual; to minimise this variability only medium sized individuals were measured. Because of the variability, characters cited above are of minimal use for identifications. Each species possesses a unique and distinctive rib morphology, as opposed to rib number, which allows positive identification. Because of this, rib morphology is used here as the primary criterion for identification and the other characters are used to confirm the identification.

Rib morphology is elaborate in the cardiids examined here, and there are numerous possible combinations and variations. A detailed description would be too long and involved to understand. Accordingly, descriptions have been simplified, and reference is made to the large scale photographs. The descriptions will include two parts: firstly, structure (or profile) of the ribs and secondly, their ornamentation. Rib morphology is further complicated because it differs in various parts of the shell. Two types of variation occur on a single shell. Lateral changes follow the direction of the growth lines. To describe them, the shell will be divided into four quarters: AQ = anterior quarter, MAQ = medio-anterior quarter, MPQ = medio-posterior quarter and PQ = posterior quarter. These changes are often abrupt between MPQ and PQ, but are generally gradual within a quarter or between two adjacent quarters. The PQ, then the MPQ, are the most typical quarters so descriptions begin at the PQ. Secondly, there are changes along the ribs, from the umbo to the ventral margin. To describe these variations, the shell is divided into two parts, a "juvenile" part, corresponding to the early shell near the umbo, and an "adult" part corresponding to the newer shell near the ventral margin. The longitudinal changes are always gradual. Nevertheless, the juvenile sculpture generally remains practically unchanged for the first few centimetres from the umbo. Adult morphology is variable within an individual. The process, or style, of change is constant and becomes an element as important as the morphology itself in the characterisation of the species.

Because of the uniformity of rib morphology within a species it is not necessary to have a lot of material to recognise the presence of a species in a sample of shells, one valve, even a fragment, can be sufficient. Consequently only a few specimens are needed to define new species or subspecies.

Systematics

Family Cardiidae Lamarck, 1809

Subfamily Trachycardiinae Stewart, 1930

Genus *Vasticardium* Iredale, 1927

Type species: *Cardium elongatum* Bruguière, 1789; OD Iredale 1927: 75.

Diagnosis: Shell medium to large-sized, ovoid and symmetrical to asymmetrical and posteriorly expanded, obliquely or not, "winged" or truncated. Variably but moderately elongated and inflated. 30–40 ribs, exceptionally 45. Hinge line moderately angled. Cardinal teeth in right valve separated or merely touching at their base and never connected by a high and narrow dorsal saddle. Ribs enlarge quickly in juvenile median and anterior parts, square-sided and fully ornamented, directly following small smooth very early shell. In PQ, ribs always high and square-sided in juvenile shells, always simple, not divided into two parts; top scales or nodules always arranged in a single row along the apex. In other quarters of adult shells, ribs generally high, often squared and overhanging interstices, rarely triangular, often bearing scales or tubercles in MPQ with crenulated margins, cross-bars in anterior half. Interstices rather deep and wide, with a flat bottom, smooth or finely striated independently of flanks of ribs, never hollowed.

Remarks: Three generic names have been utilised for the large Trachycardiinae from the Indo-West Pacific: *Trachycardium* Mörch, 1853 [Type species *Cardium isocardia* Linné; SD von Martens, 1870: 586], *Acrosterigma* Dall, 1900 [Type species *Cardium dalli* Heilprin, 1877; OD], and *Vasticardium* Iredale, 1927. In previous papers (Vidal, 1991, 1992, 1993) I used *Acrosterigma*. However, the subfamily is in need of generic revision, particularly in the Indo-Pacific where some thirty species have not been covered in recent monographs. I have now concluded that *Acrosterigma* is not appropriate for the large Indo-Pacific Trachycardiinae, and follow Iredale (1927) in recognising *Vasticardium*. *Acrosterigma* is now restricted to some American Recent and fossil species and to several smaller Indo-Pacific species.

Group of *Vasticardium orbita* (Broderip & Sowerby, 1833).

Diagnosis: Shell large, often asymmetrical when fully adult; MPQ often transversally expanded, PQ often winged; posterior part rarely appreciably truncated. Lunule large and well delineated with raised margins of shell forming a double wall in its axis. Basement of anterior tooth in both valves characteristically pointed and "hooked" and particularly large and prominent, with a straightened internal limit. In juvenile median and anterior part of the shell, ribs high with subtriangular, slightly rounded smooth top, with edges crenulated by regularly set successive nodules and slightly overhanging interstices which are regularly and finely striated independently of flanks of ribs which are smooth (about two striae versus one marginal nodule); in adult median part, frequent herringbone structures formed by the top rugae.

Remarks: The "hooked" character of the anterior lateral teeth (see examples pl. 1, figs. 2 and 4b or pl. 3, fig. 4b) is a distinctive feature of this group, never present in any other large Trachycardiinae. The rib morphology of the juvenile median part is also very typical of the group.

Vasticardium orbita (Broderip & Sowerby, 1833)

Cardium orbita Broderip & Sowerby, 1833: 83.

Diagnosis: Shell very large, reaching 125 mm in height, moderately elongated and variably depressed (Table 6). Subequilateral, ribs straight in projection on plane separating both valves (and not curved

Table 1.   Comparison of rib morphology of two subspecies of *Vasticardium orbita* (Broderip & Sowerby, 1833).

	V. orbita philippinense		*V. orbita orbita*
PQ	Ribs low, wide, flat or slightly concave	PQ	Ribs high, square-sided, edges overhanging
	Interstices(i)** thin, narrow		Interstices narrow, deep, flat
	Main scales(s) slightly twisted to tubercule, short, or forming thin posterior wall (w) on rib.		Main scales almost straight on posterior half of rib top.
	Anterior marginal thin, slanted scales frequent.		No anterior marginal scales.
MPQ	Contrast with PQ variable.	MPQ	Contrast with PQ weak.
	Ribs low, flat-rounded, rarely slightly overhanging.		Ribs high, trapezoidal, flat topped, sharp overhanging edges.
	Interstices very narrow		Interstices narrower than ribs
	Top main scales AOS* or AT but can be absent.		Top scales derived from marginal crenulations sharp edges overhanging.
	Interstices very narrow, wider onwards.		Interstices narrower than ribs.
	Top main scales = AOS* or AT* frequent, but can be absent.		Possible top scales derived from marginal crenulations (= not AOS)
	Anterior margin crenulations (cr) present or absent		Numerous anterior marginal crenulations, oblique, prickly.
	Posterior marginal crenulations (cr) present or absent		Strong posterior marginal crenulations oblique, prickly.
MAQ	Ribs medium, rounded to squared becoming sharp-edged onwards.	MAQ	Ribs high, trapezoidal, sharp crenulated edges, top flat.
& AQ	Marginal oblique, crenulations lengthen, form open herringbone and onwards curved rugae.	& AQ	Marginal oblique, crenulations progressively join, form herringbone, then onwards curved rugae.

* AOS, AT: Additional oblique scales (or tubercles): homologous in MPQ of the main top scales of PQ, in addition to the posterior marginal crenulations, but not derived from them. ** i,s,w,cr these initials refer to pl. 3, fig. 1.

backwards). Often "winged" (posterior half of PQ flared out, like a wing); winging often accentuated by a slightly concave radial zone between MPQ and PQ, also detectable in margin. External colour with red brown to purple more or less concentrical irregular splashes on a whitish or beige background. Internal margin always coloured in dark purple. Mean rib number 42.2, range 36–50. Rib morphology variable according to the subspecies.

Distribution and subspecies: Four geographical subspecies of *Vasticardium orbita* can be recognised: *Vasticardium orbita orbita* from southeastern Polynesia (Cook Is., Society Is., Tuamotu Is., Pitcairn I.); *V. orbita hawaiiensis* from the Hawaiian Islands; *V. orbita mendanaense* from the Marquesas; and *V. orbita philippinense* from other parts of the tropical western Pacific (Philippines, eastern Indonesia, Papua New Guinea, Micronesia, northwestern Polynesia, Melanesia, northern Queensland and northwestern Australia). *V. orbita* is replaced by *V. luteomarginatum* in the Indian Ocean (Christmas I. and northwestern Australia excepted, see below).

<p style="text-align:center;">*Vasticardium orbita orbita* (Broderip & Sowerby, 1833)</p>

<p style="text-align:center;">Pl. 1, figs. 1, 2, 3a–b.</p>

Cardium orbita Broderip & Sowerby, 1833: 83. Sowerby, 1834: fig. 13.

Laevicardium (Trachycardium) philippinense (Deshayes) Shirley *sensu* Fischer-Piette, 1977: 49, pl. 3, fig. 4 & pl. 4, Fig. 1. [Not *V. orbita philippinense* (Hedley)].

Table 2. Comparison of rib morphology of two subspecies of *Vasticardium orbita* (Broderip & Sowerby, 1833).

	V. orbita mendanaense		*V. orbita hawaiiensis*
PQ	Ribs very high, flat topped, sharp, edges overhanging.	PQ	Ribs slightly high, square-sided, edges rather smooth.
	Interstices as wide or wider than ribs.		Interstices narrower than ribs.
	Main scales slightly twisted on most of top.		Main scales twisted to conical on all of rib top, ventrally straighter.
	No anterior marginal crenulations, only festoons.		No anterior marginal crenulations festoons rare.
MPQ	Contrast with PQ strong.	MPQ	No contrast with PQ.
	Ribs very high, asymmetrical, trapezoidal overhanging, rather smooth edges.		Ribs high, triangular, flat-top, sharp edges.
	Interstices wider than ribs.		Interstices as wide as ribs.
	No main scales, top smooth.		Top main scales twisted or conical as in PQ (=AOS).
	Numerous anterior marginal crenulations, oblique, prickly.		Numerous anterior marginal crenulations, oblique, prickly.
	Strong posterior marginal crenulations, oblique, prickly.		Numerous posterior marginal crenulations, herringbone with AOS, disappearing.
MAQ	Ribs very high, trapezoidal, sharp, crenulated edges, top flat.	MAQ	Ribs high, round-triangular to squared, edges crenulated.
& AQ	Marginal oblique crenulated, progressively join form herringbone, then onwards curved rugae.	& AQ	Asymmetrical herringbone top rugae become progressively straight then curved.

* AOS, AT: Additional oblique scales (or tubercles): homologous in MPQ of the main top scales of PQ, in addition to the posterior marginal crenulations, but not derived from them.

Table 3 – DISTRIBUTION of *VASTICARDIUM ORBITA* and *VASTICARDIUM LUTEOMARGINATUM*

V. ORBITA
1 ★ *V. orbita orbita*
2 ✳ *V. orbita hawaiiensis*
3 ✻ *V. orbita mendanaense*
4 ▲ *V. orbita philippinense*

V. LUTEOMARG.
5 ● *V. luteomarg. luteomarg.*
6 ■ *V. luteomarg. marerubrum*
7 ◆ *V. luteomarg. insulare*

PL1

1

2

3a

4a

4b

3b

5

4c

PQ

MPQ PQ
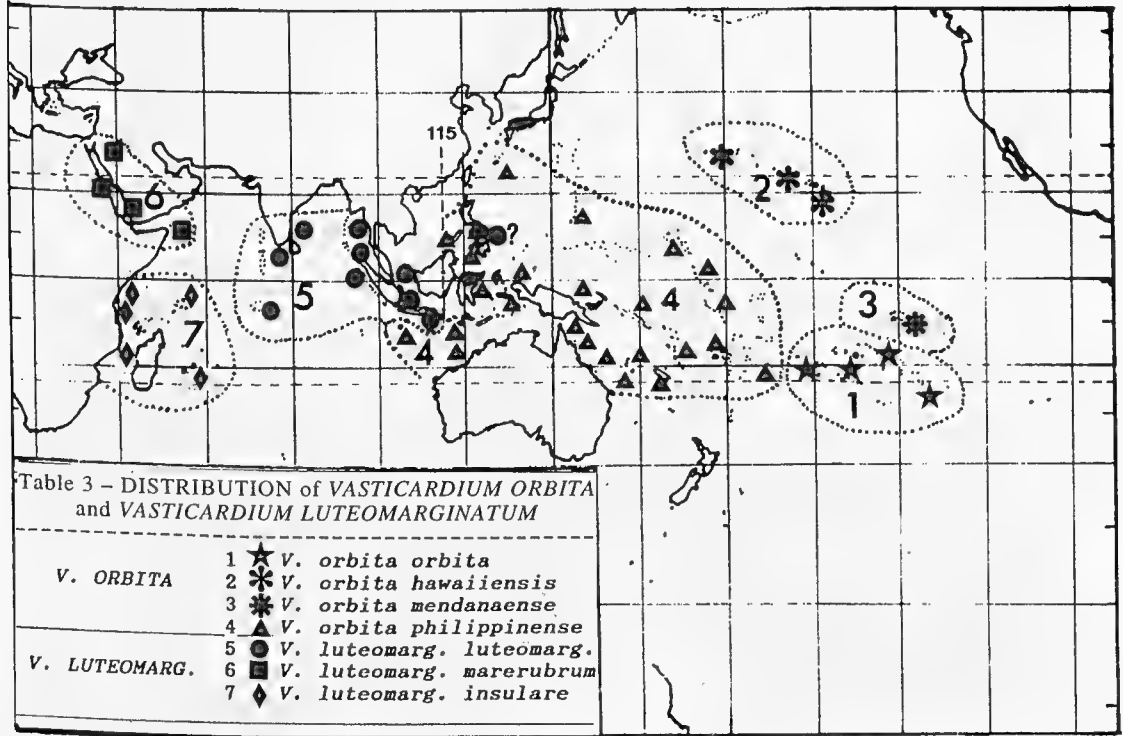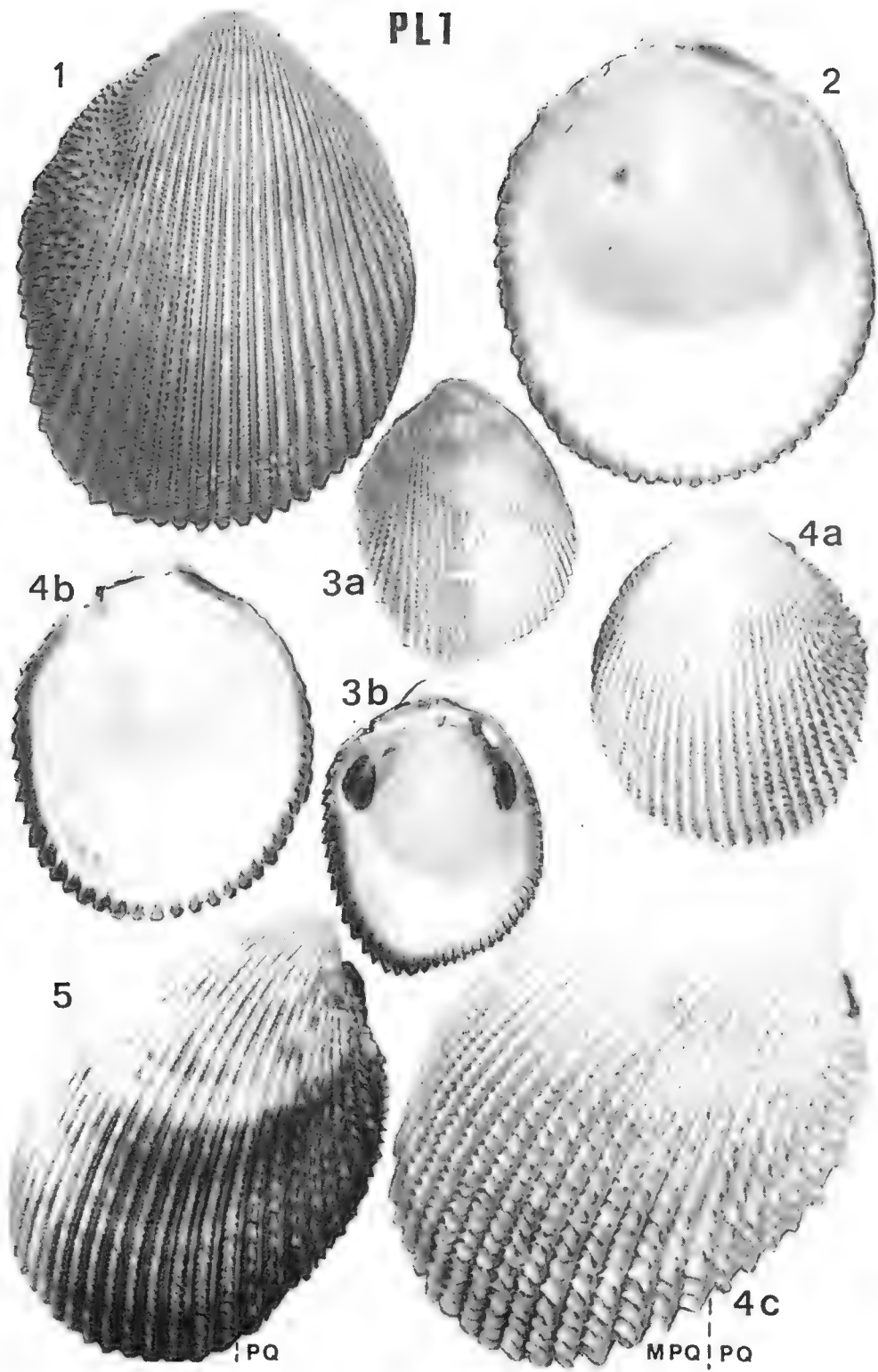
Types: Three syntypes in BM(NH), Cuming's collection, uncatalogued, from Anaa Island, Polynesia. The largest specimen is figured by Sowerby (1834: fig. 13) and Reeve (1845: fig. 85) and here (pl. 1, fig. 1).

Diagnosis: By far the largest subspecies (height up to 125 mm); adult shell thick and heavy. Young specimens about equilateral and ovoid; fully adult shells less equilateral (a little truncated and winged in PQ), and appreciably elongated (lengthening due to an expansion limited to MPQ, which protrudes in the ventral margin (pl. 1, fig 3a–b)). Colour beige with red-brown to purple splashes more abundant in posterior half, sometimes entirely darker coloured. Mean number of ribs 45.4 (range 41–50). Ribs are straight in projection, sometimes a little curved forwards, even in the largest shells. See Table 1 for rib morphology of adult shell.

Measurements:

	Height (mm)	Length (mm)	Width (mm)	L/H	W/L	Ribs
Syntypes [BM(NH)]	83.0	64.0	58.3	0.77	0.91	42
	72.5	58.6	48.3	0.81	0.82	45
	38.4	33.4	26.0	0.87	0.78	44
POLYNESIA,Tuamotu[MNHN]	124.4	94.0	86.9	0.76	0.92	46
POLYNESIA,Tuamotu[MNHN]	124.5	92.1	(82.0)	0.74	0.89	46
POLYNESIA,Gambier[MNHN]	121.5	89.9	83.2	0.74	0.93	50
POLY.,Tahiti[USNM879726]	77.4	59.2	(52.6)	0.76	0.89	44
PITCAIRNS[USNM731901]	81.6	64.0	(53.6)	0.78	0.84	48
COOK,Mauke[UGML BMAK71]	76.1	60.8	(49.0)	0.80	0.81	47
COOK,Rarot.[UGMLBRAR118]	69.4	56.6	46.6	0.82	0.82	47

Other specimens:
1 – Morphometric data range: 42.7–121.2, 36.3–86.0, 27.0–85.0, 0.71–0.89, 0.74–0.99 (13 measured in 12 lots)
2 – Rib counts (18 counted in 15 lots): 41–50

General mean morphometric ratios, shells H over 65.0: 0.78, 0.88 (14 measurements in 12 lots) S.D.: 0.034, 0.050

General mean rib number (28 counts in 27 lots): 45.4 S.D.: 2.01

Material examined: The type specimens – Other lots: Polynesia: Tahiti : 1(MNHN), 2(USNM); Moorea 1(LACM); Tuamotu: Hao: 1(MNHN); Aratica: 1(MNHN); Anaa: 1(MNHN), 1(ZMA)– Pitcairn: 2(USNM)– Cook: Aitutaki: 4(UGML); Rarotonga: 2(UGML); Mauke: 2(UGML). Pacific Ocean: 2(MNHN), 1(IRSNB), 1(MHMV); No Locality: 2(MNHN), 1(ZMA), 1(AMS), 1(BM(NH)).

Distribution: Three Polynesian ridges: Cook Is., Society Is., and Tuamotu Is.

Remarks: *V. orbita orbita* is distinguished from the other subspecies by its greater number of ribs, shell shape, often its large dimensions and weight. The mean morphometric ratios are different, with the shell more elongated and more globose (Table 6). The shortness of the posterior scales on the ribs in the PQ, and the absence of twisted or conical scales in the MPQ separate it from *hawaiiensis*; *mendanaense* is smaller and more vividly coloured, has higher ribs and wider interstices in the PQ

Plate 1. Figure 1. Syntype of *Cardium orbita* figured by Sowerby. BM(NH). L= 64.0mm. Figure 2. Another syntype of *Cardium orbita*. BM(NH). L= 58.6mm. Figure 3a–b. *Vasticardium orbita orbita*. Very large specimen from Tuamotu Archipelago. MNHN, Coll. Vidal. L= 92.1mm. Figure 4a–c. *Vasticardium orbita hawaiiensis*. Specimen from Kaneohe Bay, Oahu, Hawaii. 4c. PQ and MPQ zones. MNHN, Coll. Burgess. L= 48.0mm. Figure 5. *Vasticardium orbita mendanaense*. Specimen from Nuku Hiva Is, Marquesas, PQ and MPQ zones. MNHN, coll. Vidal. L= 39.1mm.

and MPQ, and only rarely has short oblique scales in the MPQ; *philippinense* differs by rib morphology (in particular *philippinense* usually has numerous AOS or AT in the MPQ combined with separate marginal crenulations which do not exist in the nominal subspecies, where the straight and oblique scales of the MPQ result from the modification of the posterior marginal crenulations).

It is difficult to understand why Fischer-Piette (1977: 30) synonymised *C. orbita* with *C. flavum* Linné.

Vasticardium orbita hawaiiensis (Dall, Bartsch & Rehder, 1938)
Pl. 1, figs. 4a–b–c and pl. 4, fig. 3.

Trachycardium hawaiiensis Dall, Bartsch & Rehder, 1938: 155, pl. 41, figs. 1–4.

Trachycardium orbita (Sowerby, 1833): Kay, 1979: 556.

Type: Holotype USNM 337390, from Keaukaha, Hilo, Hawaii.

Diagnosis: Shell generally medium-sized for group, but some specimens can reach 90mm or more. Shape generally ovoid and roughly equilateral, sometimes mildly asymmetrical. Rarely strongly winged in the PQ. Moderately elongated and globose. See Table 2 for rib morphology of adult shells.

Measurements:

	Height (mm)	Length (mm)	Width (mm)	L/H	W/L	Ribs
Holotype[USNM337390]	68.5	55.2	44.8	0.81	0.81	42
Kay's 1979 specimen	65.0	53.0	40.0	0.82	0.75	42
Oahu [MNHN]	59.3	48.2	40.0	0.81	0.83	37
Oahu [MNHN]	58.5	48.0	40.0	0.82	0.83	38
Oahu [MNHN]	57.8	45.3	37.2	0.78	0.82	36
Oahu [MNHN]	55.5	46.0	35.1	0.83	0.76	38
Oahu [MNHN]	50.2	42.2	31.0	0.84	0.73	38
Oahu [MNHN]	47.4	38.3	35.3	0.79	0.92	40
Pearl & Herm[USNM428416]	58.7	50.0	42.5	0.85	0.85	43
Midway[USNM428434]	70.0	54.4	49.0	0.78	0.90	41

Other specimens:
1 – Morphometric data   range: 22.5– 91.8   19.6– 72.8   15.8– 65.0   0.76– 0.85   0.78– 1.03
    (13 measured in 13 lots)
2 – Rib counts (20 counted in 20 lots): 38–44

General mean morphometric ratios, shells H over 45.0:   0.81   0.82
    (16 measured in 13 lots)   S.D.: 0.02   0.06
General mean rib number (30 counted in 26 lots): 41.0   S.D.: 1.89

Material examined: Lots: Hawaii: 1(NHMW), 2(LACM), 1(BISHOP); Oahu: 2(MNHN), 1(USNM), 8(LACM), 6(BISHOP); Maui: 2(MNHN), 3(LACM), 2(BISHOP), 1(USNM); Kauai: 2(LACM), 1(USNM); Mokuoloc: 1(AMS); Pearl & Hermes Reef: 1(USNM), (3BISHOP); Midway: 1(USNM), 1(BISHOP); no loc.: 1(MNHN); Other islands: 6(BISHOP).

Distribution: This subspecies is endemic to the Hawaiian Islands.

Remarks: *V. orbita hawaiiensis* is separated from the nominal subspecies by its more regular ovoid shape and smaller number of ribs and from the other subspecies by the presence of wide twisted scales or conical ornamentation both in the PQ and the MPQ of the adults, without any contrast between these two zones.

Vasticardium orbita mendanaense (Sowerby, 1897)
Pl. 1, fig.5 and pl. 2, figs. 1a–b.

Cardium mendanaense Sowerby, 1897: 138, pl. 11, fig. 3.

Type: Holotype BM(NH) 1897.4.30.4, from Marquesas, Thomas collection (pl. 2, figs. 1a–b).

Diagnosis: Smallest of the subspecies; shape generally equilateral and ovoid with rarely a small posterior truncation and winging. Moderately elongated and rather globular. Vividly coloured in adult part of shell with large brown-purple splashes. Posterior part always entirely purple. Internal margin brown-purple. Ribs straight in projection or even a little curved. See Table 2 for rib morphology of adult shells.

Measurements:

	Height (mm)	Length (mm)	Width (mm)	L/H	W/L	Ribs
Holotype[BM(NH)1987-4-30-4]	61.2	52.1	45.0	0.85	0.86	39
Marquesas [MNHN]	61.2	49.5	41.5	0.81	0.84	40
Marquesas [MNHN]	63.5	56.2	52.0	0.89	0.93	39
Marquesas,NukuHiva[MNHN]	49.8	42.0	(34.0)	0.84	0.81	39
Marquesas,NukuHiva[MNHN]	46.0	39.1	(30.0)	0.85	0.77	40
Marquesas[ANSP156209]	63.0	52.7	(42.2)	0.84	0.80	40
Marquesas[USNM700277]	51.2	44.8	37.4	0.87	0.83	40
Marquesas[USNM799407]	43.6	36.4	28.3	0.83	0.78	39
Marquesas[USNM790457]	42.7	35.2	(30.0)	0.82	0.85	39
Marquesas[ANSP315633]	40.5	34.7	29.2	0.86	0.84	37

Other specimens:
1 – Morphometric data   range: 33.5–   8.0–   22.0–   0.82–   0.73–
        (9 measured. in 6 lots)   51.6   43.0   36.0   0.88   0.84
2 – Rib counts (11 counted in 8 lots):   37–43

General mean morphometric ratios, shells H over 40.0:   0.85   0.82
        (16 measured in 9 lots)   S.D.: 0.02   0.03
General mean rib number (21 counted in 11 lots): 39.4   S.D.:   1.01

Material examined: The holotype. Other lots: Polynesia: Marquesas: 3(MNHN), 2(ANSP), 1(IRSNB), 3(USNM), 1(LACM), 4(BISHOP).

Distribution: This subspecies is endemic to the Marquesas.

Remarks: *V. orbita mendanaense* is easily separated from *V. orbita orbita* and *V. orbita hawaiiensis* by its smaller dimensions, darker colours, strong contrast between PQ and MPQ. It differs from *V. orbita philippinense* mainly by its high ribs and wide interstices in the posterior half of the shells.

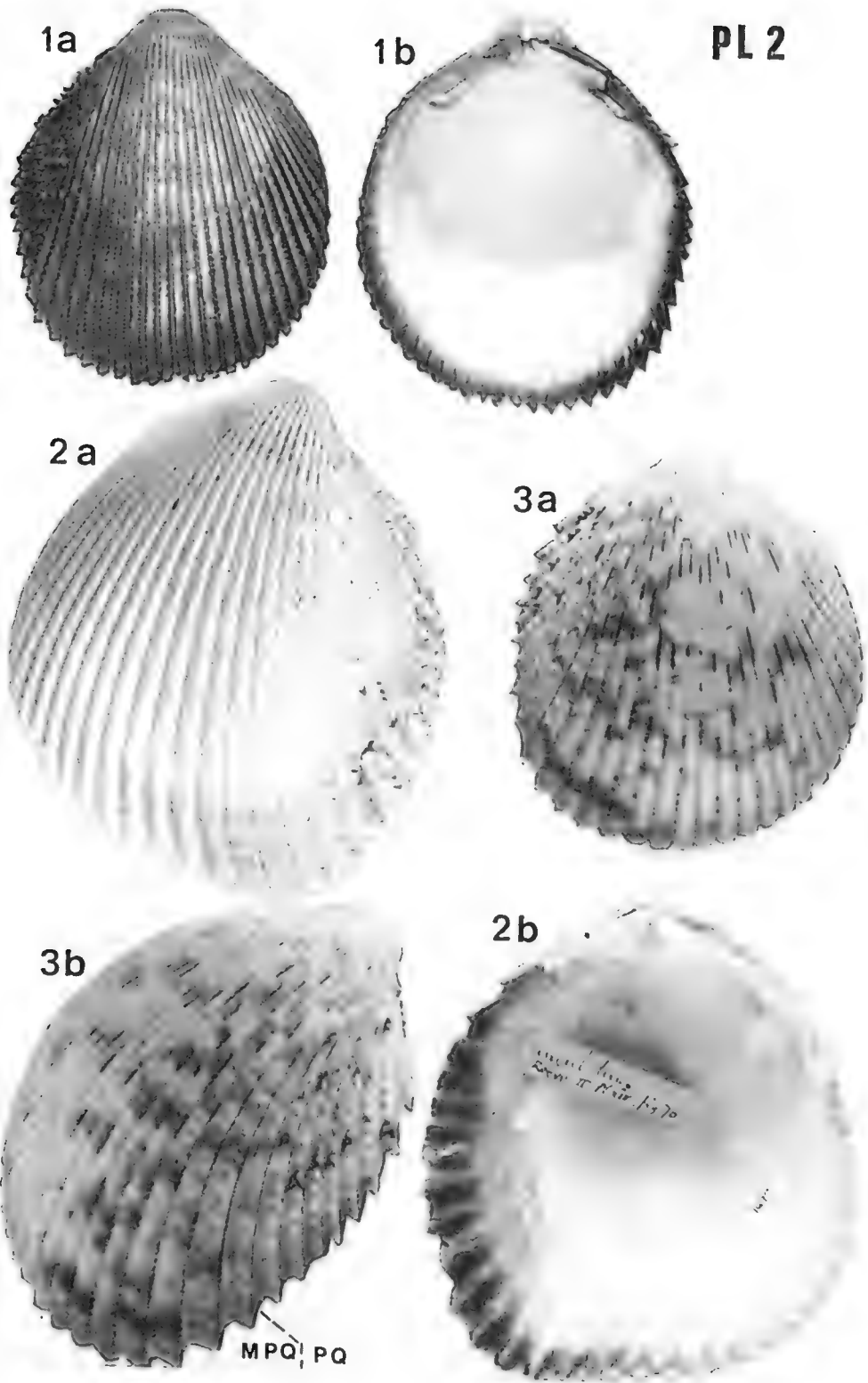## *Vasticardium orbita philippinense* (Hedley, 1899)
Pl. 2, figs. 2a–b, 3a–b, and pl. 3, figs. 1, 2.

Cardium angulatum Lamarck *sensu* Reeve 1845: Sp. 70, fig. 70. [Not *Cardium angulatum* Lamarck, 1819].

Cardium philippinense Deshayes: Hedley 1899: 503.

Cardium (Trachycardium) pseudoangulatum Bülow, 1905: 79, pl. 1, fig. 3.

Cardium philippinensis Deshayes: Shirley, 1912: 95.

PL 2

MPQ PQ

Trachycardium orbita (Sowerby): Wells *et al.* 1990: pl. 78, fig. 368.

Acrosterigma mendanaense (Sowerby) *sensu* Lamprell & Whitehead 1992, pl.29, fig. 188. [Not *V. orbita mendanaense* (Sowerby)]

Types: According to article 72(b) of the Code, the type of *Cardium philippinense* is the shell figured by Reeve as *Cardium angulatum* Lamarck: 1845, fig. 70, UMZ, No 1694, Saul coll., locality unknown (see pl. 2, figs. 2a–b). The type of *C. pseudoangulatum* is the specimen figured by Bülow, not traced, unknown locality; recorded dimensions: H = 95 mm, L = 80 mm, with 38 to 40 ribs.

Diagnosis: Rather large-sized, up to 107.5 mm in height. Shell more or less equilateral, but generally asymmetrical in shape with a straightening in the AQ and a winging in PQ. Another straightening may occur on the ventral margin: its combination with adjacent PQ truncation makes a rough angle in the margin. Reeve's specimen (1845: fig. 70) is abnormally angulated in this way. Moderately elongated, and rather depressed (the most of all subspecies, see Table 6). Colour always beige with brown-purple, irregular, more or less concentric splashes, often darker in interstices, and more abundant in MPQ. In PQ, presence of short squared dark brown stains. Internal margin dark purple, rarely partially yellow. Ribs often straight in projection, even in asymmetric forms, but specimens with an oblique expansion of the MPQ with ribs turning backwards (characters of *Vasticardium luteomarginatum*) occur. See Table 2 for rib morphology of adult shells.

Measurements:

	Height (mm)	Length (mm)	Width (mm)	L/H	W/L	Ribs
Type specimen[UMZC1694]	107.3	90.5	70.2	0.84	0.78	36
Philippines[BM(NH),Deshayes]	91.5	78.0	58.0	0.85	0.74	40
Mariana[WAM 3–73]	90.0	73.1	58.0	0.81	0.79	44
Cook, Niue[UGML,BNIUE171]	90.0	72.7	60.8	0.81	0.84	39
Vanuatu, PortVila[MNHN]	88.4	74.0	58.6	0.84	0.79	39
Solomon [QM]	98.1	84.0	69.3	0.86	0.82	41
PNG, Madang[WAM 40–95]	83.3	70.0	55.7	0.84	0.80	40
N.Qld,Spur Rf[AMSC92097]	102.2	82.5	69.3	0.81	0.84	42
WA,Ashmore Rf[WAM 43–95]	65.0	57.6	39.1	0.89	0.68	40
WA,Christm.Is[AMSC144509]	73.0	59.0	44.6	0.81	0.76	39

Other specimens:

1 – Morphometric data range:	24.4–	20.9–	15.6–	0.74–	0.69–	
(61 measured in 43 lots)	107.5	87.3	66.4	0.91	0.87	

2 – Rib counts (73 counted in 55 lots): 36–44

General mean morphometric ratios, shells H over 60.0:

				0.83	0.78	
(44 measured in 30 lots)			S.D.:	0.033	0.048	

General mean rib number (83 counted in 65 lots): 40.0   S.D.: 2.01

Material examined: The holotype. Other lots: Indonesia: Lombok: 1(ZMA), 1(NNM); Sulawesi: 1(NNM); Moluccas: 2(ZMA); Irian Jaya: 2(ZMA)– Malaysia: Sabah 1(ZMA)– Philippines: 3(LACM), 1(BM(NH)), 2(MNHN), 1(ANSP), 1(MNHN)– Japan: Okinawa: 3(LACM), 1(BISHOP)– Guam: 6(UGML)– Papua New Guinea: Port Moresby: 1(NNM); Hansa Bay: 5(IRSNB)– Solomon: 1(ZMA), 1(LACM), 1(QM)– Marshall: Majuro: 1(UGML)– Kiribati: Tarawa: 1(UGML)– Tuvalu:

Plate 2.   Figure 1a–b. Holotype of *Cardium mendanaense*. BM(NH). L= 52.1mm. Figure 2a–b. Holotype of *Cardium philippinense* Hedley [= Shell figured by Reeve (1845: fig 70) as *Cardium angulatum* Lamarck]. UMZ coll. Saul. L= 90.5mm. Figure 3a–b. *Vasticardium orbita philippinense*. Specimen from Cebu, Philippines. 3b. PQ and MPQ zones. MNHN, coll. Vidal. L= 58.0mm.

Funafuti: 1(AMS)– Niue: 4(UGML)– Tonga: 1(BM(NH))– Fiji: 1 (UGML), 1(LACM)– Vanuatu: Port Vila: 1(MNHN), 1(LACM); Malecula 1(MNHN)– New Caledonia: Lifou: 1 subfossil (AMS); Passe de Boulari: 1(Private coll.); Koumac: 1(MNHN); Chesterfield Is: 5(MNHN)– Australia: Queensland and North Queensland: 5(AMS), 2(QM); Swain reef: 1(QM); Western Australia: 1(LACM), 1(IRSNB), 2(WAM); Christmas Is: 1(AMS), 2(WAM). Typical specimens of this subspecies are present in the late Miocene–Pliocene fossil reef of Niue Is. One large bivalve specimen, several valves and fragments, collected by G. Paulay, UGML, have been examined.

Distribution: Intertropical western Pacific Ocean. *Vasticardium orbita philippinense* is totally absent west of 115°East (Christmas I. excepted), where it is replaced by *V. luteomarginatum* (see discussion below).

Remarks: *V. orbita philippinense* differs from the other subspecies primarily in rib morphology (ribs very low and flat, sometimes concave in PQ, with reduced scales and very narrow interstices; ribs low in MPQ with more or less spaced AOS, interstices narrow), and shell morphometry (more depressed, see Table 6).

The name *Cardium philippinense* was first introduced by Hedley (1899: 503), based on several specimens in BM(NH) hand labelled by Deshayes with this name, in synonymy of *C. angulatum* Lamarck, with reference to Reeve (1845, Sp. 70). Reeve's illustration qualifies as an indication under article 12(b)(7) of the Code. More recently, the name *philippinense* has been treated as a valid species by Shirley (1912: 95) and Tomlin (1934: 84), and this action makes it an available name under articles 11(e) and 50(g) of the Code. Accordingly I use the name *philippinense* as the valid name for the western Pacific populations of *V. orbita*. The alternative would have been to use the name *V. pseudoangulatum* (Bülow, 1905), a name that was never used following its publication until it was cited by Vidal (1991) and used by Voskuil & Onverwagt (1991). Considering this very limited usage, there is no reason why the Principle of Priority should not apply. Hedley's usage of the name *"philippinense* Deshayes" is based on material so labelled in the BM(NH). Under articles 9(g) and 50(g) of the Code, Hedley, not Deshayes, is the author of the name.

Vasticardium luteomarginatum (Voskuil & Onverwagt, 1991)

Trachycardium luteomarginatum Voskuil & Onverwagt, 1991: 61, pl. 2, fig. 4 [not figs. 5–6].

Diagnosis: Shell large to very large, reaching 100 mm in length, moderately elongated and rather depressed. Generally inequilateral when adult, with oblique expansion of posterior part and curving of ribs backwards in projection; rarely winged, posterior dorsal margin almost always tilted. Mean rib number 32.5, range 29–36. External colour beige to orange-yellow or pinkish, with darker splashes or stripes, MPQ often darker; internally white with margin strongly coloured yellow-orange, rarely purple. See Table 4 for rib morphology of adult shells.

Distribution and subspecies: Three geographical subspecies of *Vasticardium luteomarginatum* are recognised: *Vasticardium luteomarginatum luteomarginatum* in the northeastern tropical part of the Indian Ocean, Andaman Sea, coasts of Sumatra and Java; *V. luteomarginatum marerubrum* in the Red Sea, Gulf of Aden and northern coast of Somalia; and *V. luteomarginatum insulare* in the southwestern part of the tropical Indian Ocean. The origin of rare isolated specimens from outside this range is considered dubious and needs confirmation (see discussion below).

Remarks: When they described *T. luteomarginatum* as a new species, Voskuil & Onverwagt overlooked or ignored the name *Cardium ignotum* Jousseaume in Lamy 1927. However, this name presents several nomenclatural difficulties, and it is necessary to present here a translation of the paragraph where this name is introduced:

"Born has described (1870, Test. Mus. Caes. Vindob., p. 46, pl. 3, fig. 6–7) *C. leucostoma*, to

Table 4.   Comparison of the adult rib morphology of *V. luteomarginatum marerubrum*, *V. luteomarginatum insulare* and *V. luteomarginatum luteomarginatum*.

	V. luteomarginatum marerubrum	V.luteomarginatum insulare	V. luteomarginatum luteomarginatum
PQ	Ribs slightly low, wide and flat, edges vary from sharp to smooth. Interstices deep, wide.	Ribs slightly low, wide and flat, edges sharp. Interstices deep, wide.	Ribs very low very flat, sometimes slightly concave, margins smooth. Interstices shallow and very narrow.
	Posterior main oblique scales long.	Posterior main oblique scales short.	Posterior main scales very small forming thin strip or scar line.
MPQ	Anterior marginal crenulation persistent.	Anterior marginal crenulation persistent.	No anterior marginal crenulations.
	Ribs squared, margin sharp, overhanging.	Ribs slightly squared, top rounded, margin variable, overhanging or not.	Ribs low, flat-rounded becoming triangular, edges smooth.
	Interstices wide. No AOS* nor AT*.	Interstices wide. AOS or AT frequent in the whole zone.	Interstices narrow, becoming wider. AOS or AT possible, forming a triangular zone in medium aged part.
	Strong anterior marginal crenulations present. Posterior marginal crenulations present.	Anterior marginal crenulations disappearing. Posterior marginal crenulations irregular.	No anterior marginal crenulations. No posterior marginal crenulations
MAQ & AQ	Ribs high, crenulated then onwards top-ridged.	Ribs high, crenulated then onwards top-ridged.	Ribs high and slightly overhanging, progressively crenulated then top-ridged.
	Herringbone structure frequent.	No herringbone structure.	No herringbone structure.

* AOS, AT: Additional oblique scales (or tubercles): homologous in MPQ of the main top scales of PQ, in addition to the posterior marginal crenulations, but not derived from them.

Table 5.   Comparison of rib morphology of *Cardium magnum* and *Vasticardium luteomarginatum* (see Pl. 4).

		magnum (fig. 9)	luteomarginatum (fig. 8)
	Ribs	Rounded and flattened, margin smooth, in continuity with interstice.	Squared, top flatly triangular, margin crenulated overhanging and independent from interstice.
	Interstices	Rounded, regularly grooved, grooves affecting sides of ribs.	Flat, finely striated, striae not affecting sides of ribs.

which he credited Jamaica as locality: although Römer (1869, Conch. Cab., 2d ed., p. 52) thinks this origin is erroneous and that in reality it is the Singapore form figured under this name by Reeve (1845, Conch Icon., pl. IX, fig 47 [This shell really is *T. elongatum*, as indicated by Reeve (see Vidal, 1992: 46)], and pl. XIII, fig. 47). Dr Jousseaume says that: "this Indian Ocean species has been confused by authors and is unrelated to the type [of *C. leucostoma*] figured by Born". He would have proposed for it the name *C. ignotum*, if he had not thought that *C. subrugosum* Sowerby (1840, P.Z.S.L., p. 108; 1841, Conch. Illustr., p. 5, fig. 34; 1844, Reeve, Conch. Icon., pl. XI, fig. 55) might well be a juvenile of the present species, which would then have to keep that name".

Under articles 11(d) and 15 of the code, a name proposed conditionally before 1961 is available.
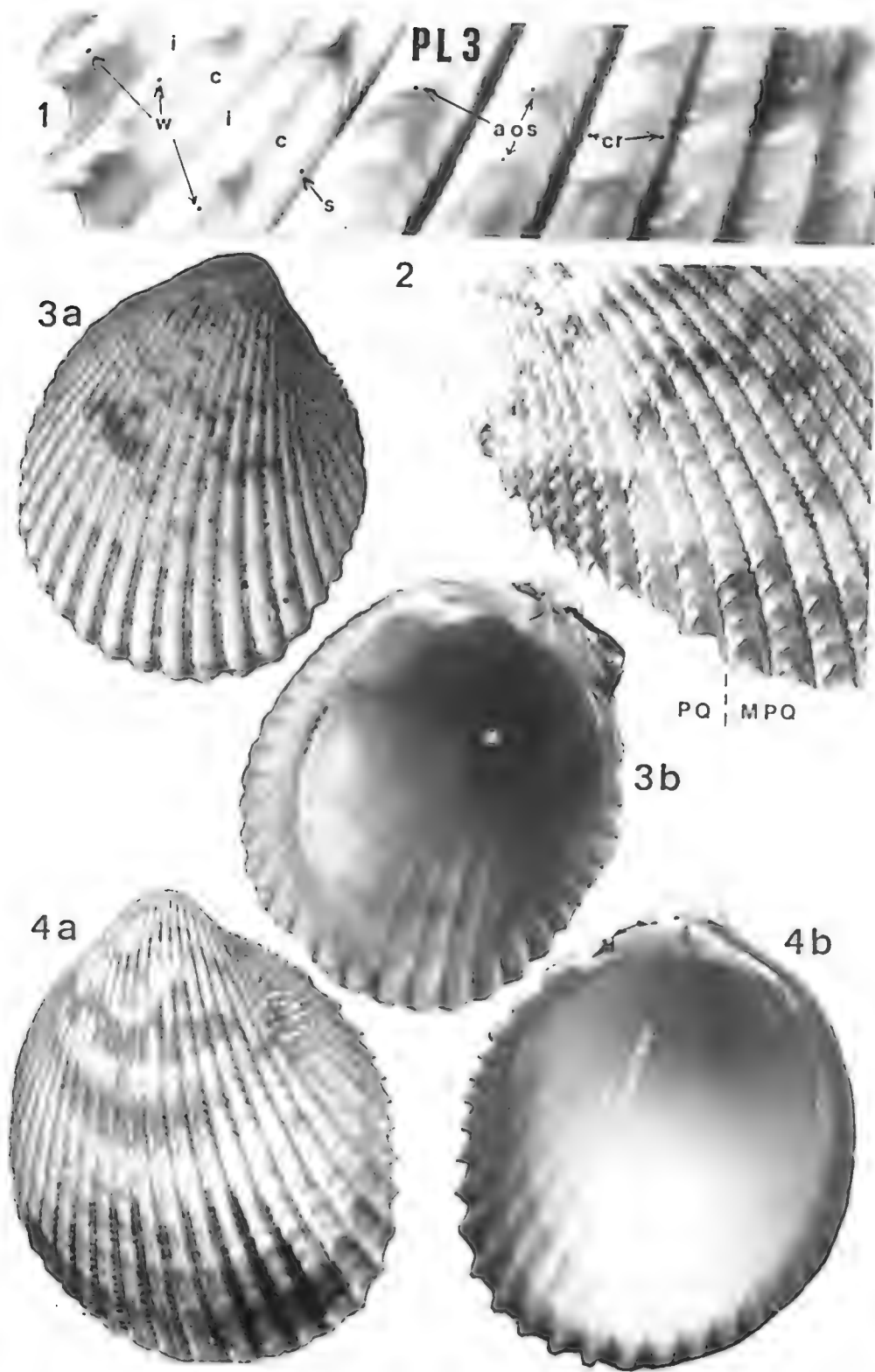
References to Reeve provide an indication in the sense of article 12(b)(7) of the code. However, strictly speaking, *C. ignotum* is not even proposed conditionally, since Lamy states that Jousseaume "would have proposed" it [which Jousseaume did not formally do]. Furthermore, Lamy is the only author who has used this name and he treats it as a synonym [of *C. subrugosum*]. Consequently, I treat *Cardium ignotum* as an unavailable name, and use the next available one, viz *T. luteomarginatum*.

Remarks: The differences with the American Atlantic species *C. leucostomum* Born, 1780 (= *C. magnum* L. *sensu* Clench & Smith, 1944), as evidenced by its holotype MHMW 857a, are numerous in rib morphology; only one, which is deciding, will be cited in the median umbonal part of juvenile shells (Table 5 and pl. 4, figs. 8 and 9):

Vasticardium luteomarginatum luteomarginatum (Voskuil & Onverwagt, 1991)

Pl. 3, fig. 4a–b, Pl. 4, figs. 1, 4, 5, 6.

Cardium marmoreum var [2] Lamarck, 1819: 9.

Cardium leucostoma Born: *sensu* Reeve, 1845: Sp. 47, pl. 13, fig. 47. [Not *C. leucostoma* Born, 1780].

Cardium ignotum Jousseaume in Lamy, 1927: 519.

Laevicardium (Trachycardium) enode (Sowerby) *sensu* Fischer-Piette 1977:62 [Not *Vasticardium elongatum enode* (Sowerby, 1840).

Trachycardium luteomarginatum Voskuil, & Onverwagt, 1991: 61, pl. 2, fig. 4 [not fig. 5–6].

Types: *Trachycardium luteomarginatum*: Holotype NNM 56777, reportedly from Samar Is, Philippines. H= 75.0 mm, L= 61.0 mm, W= 45.5 mm, with 32 ribs (pl. 3, figs 4a–b). Eight individuals cited as paratypes, all from NW Indonesia, all in the NNM: 56578, one specimen, Bay of Batavia; 56579, one left valve, NW Sumatra; 56580, two right valves and one left valve, NW Sumatra; 56581, one left valve, NE Sumatra; 56586, one right valve and one left valve, NW Sumatra. *Cardium marmoreum var* [2]: Lamarck's reference shell MHNG 1085/53, Sri Lanka. *Cardium ignotum*: As seen above the holotype of this nominal species is the shell figured by Reeve (1845, pl. 13, fig 47) from Singapore, not traced.

Diagnosis: Shell large, up to 100 mm in height. Generally slightly asymmetric, with posterior slightly expanded. Sometimes slightly truncated, but very rarely winged, although there is often a slight depression separating PQ and MPQ. Variably but never strongly elongated and moderately depressed (Table 6). In some specimens, tips of interstices in MPQ margin overlap other valve. External colour beige to orange-yellow or pinkish, with darker splashes or stripes, MPQ often darker. Internally white with margin strongly coloured yellow-orange, rarely purple. Ribs almost always curved backwards in projection. See Table 4 for rib morphology of adult shells.

Plate 3. Figure 1. *Vasticardium orbita philippinense*. Same specimen as in Plate 2, figures 3a–b, right valve; detail of PQ and MPQ zones. Scale = x 4.25. (Explanation of abbreviations is in Table 1). Figure 2. *Vasticardium orbita philippinense*. Specimen from Passe de Boulari, New Caledonia; detail of PQ and MPQ zones. Private coll., Nouméa. L= 53.7mm. Figure 3a–b. Holotype of *Trachycardium marerubrum*. NNM. L= 62.0mm. Figure 4a–b. Holotype of *Trachycardium luteomarginatum*. NNM. L= 61.0mm.

Measurements:

	Height (mm)	Length (mm)	Width (mm)	L/H	W/L	Ribs
Holotype [NNM 56577]	75.0	61.0	45.5	0.81	0.75	32
LamarckType[MHNG1085–52]						
C. marmoreum var.[2]	74.0	62.6	47.7	0.85	0.76	32
Indian Ocean [MNHN]	87.5	71.1	59.0	0.81	0.83	35
India [MNHN]	90.5	77.0	(61.0)	0.85	0.79	30
Andaman Sea [MNHN]	85.0	69.5	53.9	0.82	0.78	34
Thailand, PhuketIs[MNHN]	'84.4	70.0	54.7	0.83	0.78	34
Singapore [MNHN]	86.9	68.1	51.5	0.78	0.76	32
Singapore [MNHN]	61.3	53.1	40.5	0.87	0.76	35
Chagos,PBanhos[BMexp1978]	100.0	77.5	60.1	0.77	0.78	34
Chagos,Spur Rf.[UGML]	81.0	65.8	59.1	0.81	0.90	34

Other specimens:
1 – Morphometric data range:	44.6–	39.0–	27.8–	0.79–	0.70–
(13 measured in 7 lots)	90.0	71.0	53.0	0.86	0.83

2 – Rib counts (33 counted in 23 lots): 31–35

General mean morphometric ratios, shells H over 60.0:   0.82   0.78
    (21 measured in 13 lots)   S.D.: · 0.028   0.039

General mean rib number (43 counted in 33 lots): 32.7 S.D.: 1.43

Material examined: The holotype and the height paratypes of *T. luteomarginatum* in the NNM-Other lots: No location 1(MNHN), 1(ZMA), 2(BM(NH))– Indian Ocean 1(MNHN), 1(IRSNB), 1(MHMV)– Chagos: 1(MNHN), 1(BM(NH), 2(UGML)– India: 1(MNHN); Sri Lanka: 1(MHMV), 1(LACM), 1(BM(NH))– Nicobar: 1(NMW)– Thailand: Andaman Sea 1(MNHN); Phuket 2(MNHN), 1(LACM)– Singapore: 2(MNHN), 1(BM(NH)), 1(MHNV)– Indonesia: N. Sumatra 1(ZMA); Sabang Is 2(ZMA); Bay of Batavia 2(ZMA); W. Java 1(ZMA); Bali 1(ZMA).

Distribution: *V. luteomarginatum luteomarginatum* totally replaces *V. orbita philippinense* to the west of 115°E (Christmas Island excepted).

Remarks: *V. luteomarginatum luteomarginatum* differs from the two other subspecies by its smoother character, colouration, and rib morphology in the MPQ (ribs rounded to triangular, instead of square-sided). Adult shells are also generally larger.

Vasticardium luteomarginatum marerubrum (Voskuil & Onverwagt, 1991)
Pl. 3, figs. 3a–b and pl. 4, fig. 2.

Cardium rugosum Lamarck *sensu* Reeve, 1845: Sp. 68, fig. 68. [Not *Cardium rugosum* Lamarck, 1819].

Cardium magnum Chemnitz *sensu* Issel, 1869: 74. [Not *Cardium magnum* Linné *sensu* Chemnitz, 1782 = *Cardium angulatum* Lamarck, 1819].

Cardium ignotum Jousseaume in Lamy, 1927: 519.

·*Cardium subrugosum* Sowerby *sensu* Lamy, 1927: 519.[Not *Cardium subrugosum* Sowerby, 1838].

Cardium (Trachycardium) flavum Linné *sensu* Abrard, 1942.[Not *Cardium flavum* Linné, 1758].

Trachycardium marerubrum Voskuil & Onverwagt, 1991: 59, pl. 2, fig. 4 [not fig. 5–6].

Trachycardium enode (Sowerby, 1840) *sensu* Oliver, 1992: 126, pl. 23, figs. 5a–b.[Not *Vasticardim elongatum enode* (Sowerby, 1840)].

Types: *Trachycardium marerubrum*: Holotype NNM 56424, from S. of Giftun Is, Red Sea, Egypt (pl. 3, figs. 3a–b). Ten individuals cited as paratypes, all from the Red Sea, Egypt. Nine are in private collections, only one in the NNM 56573, one right valve.

Diagnosis: Shell medium to large-sized, reaching 93.6 mm in height, generally thick and heavy. Almost equilateral, with often a small expansion of posterior part, and with a slight curvature of ribs backwards in projection. Variably but never much elongated; variably depressed (Table 6). External colour light, white to beige, occasionally with diffuse yellowish to light brown splashes. Interior white, posterior margin white to yellowish, rarely purple. See Table 4 for rib morphology of adult shells.

Measurements:

	Height (mm)	Length (mm)	Width (mm)	L/H	W/L	Ribs
Holotype [NNM 56424]	73.5	62.0	44.9	0.84	0.72	32
Egypt, Aqaba Gulf[MNHN]	60.1	50.2	(38.0)	0.84	0.76	32
Egypt, Suez Gulf fos[MNHN]	69.2	57.0	(44.0)	0.82	0.77	34
Saudi Arabia, N.Duba[NMW]	93.6	75.5	61.7	0.81	0.82	32
Eritrea, Dahlac Is[MNHN]	71.5	58.5	(48.0)	0.82	0.82	33
Yemen, Perim Is[MNHN]	77.3	63.6	50.0	0.82	0.79	32
Red Sea,unloc.[BMNH1994–088]	72.0	59.2	50.7	0.82	0.86	32
Red Sea,unloc.[MNHN]	75.5	61.2	49.6	0.81	0.81	32
Somalia,Socotra Is[MNHN]	84.1	68.6	49.2	0.82	0.72	32
N.Mogadis[ANSP295813]	59.7	49.0	(37.2)	0.82	0.76	31

Other specimens:
1 – Morphometric data   range: 47.5– / 39.7– / 34.0– / 0.79– / 0.72–
        (26 measured in 9 lots): 81.2 / 67.5 / 52.0 / 0.90 / 0.85

	Height (mm)	Length (mm)	Width (mm)	L/H	W/L
1 – Morphometric data range:	47.5–	39.7–	34.0–	0.79–	0.72–
(26 measured in 9 lots):	81.2	67.5	52.0	0.90	0.85

2 – Rib counts (28 counted in 11 lots): 30–35

General mean morphometric ratios, shells H over 55.0:   0.83   0.78
        (32 measured in 16 lots)   S.D.: 0.025   0.041

General mean rib number (38 counted in 18 lots):32.4   S.D.:   1.02

Material examined: The holotype and one paratype of *T. marerubrum* in the NNM. Other lots: Red Sea: 3(MNHN), 4 fossil (MNHN); Gulf of Suez: 1(MNHN)– Egypt: Gulf of Suez: Raz Dib: 1 fossil (MNHN), Sharm el Bahari: 1 fossil (MNHN); Gulf of Aqaba: Gesireh Faraun: 1(MNHN)– Jordan: S. Aqaba: 1(MNHN)– Saudi Arabia: Abulatt Is: 1(MNHN); N. Duba 1(NMW)– SUDAN: Port Sudan: 1(NNM)– Ethiopia: Dahlak Archipelago: 1(MNHN)– Djibouti: Perim Is: 1(MNHN)– Somalia: Abd el Kuri Is: 1(MNHN); Socotra Is: 1(MNHN); N. Mogadishu 1(MNHN).

Distribution: This subspecies is restricted to the Red Sea, southern coast of the Gulf of Aden, and northeastern coast of Somalia. Also present in the Pleistocene raised beaches of the Red Sea.

Remarks: *Vasticardium luteomarginatum marerubrum* differs from the other two subspecies by its lighter colours, outside and inside, by its rugose shell, greater pedomorphic character and the absence of AT and AOS. From the subspecies *insulare* it differs also by not having a purple coloured internal margin.

    The light colours and the rugose aspect of this subspecies explain the erroneous identifications as *flavum, rugosum,* and *subrugosum.*
    Nardini (1937: 253, pl.17, fig.1 and 2a–b) describes both *C. rugosum* and *C. rugosum var.*

PL 4
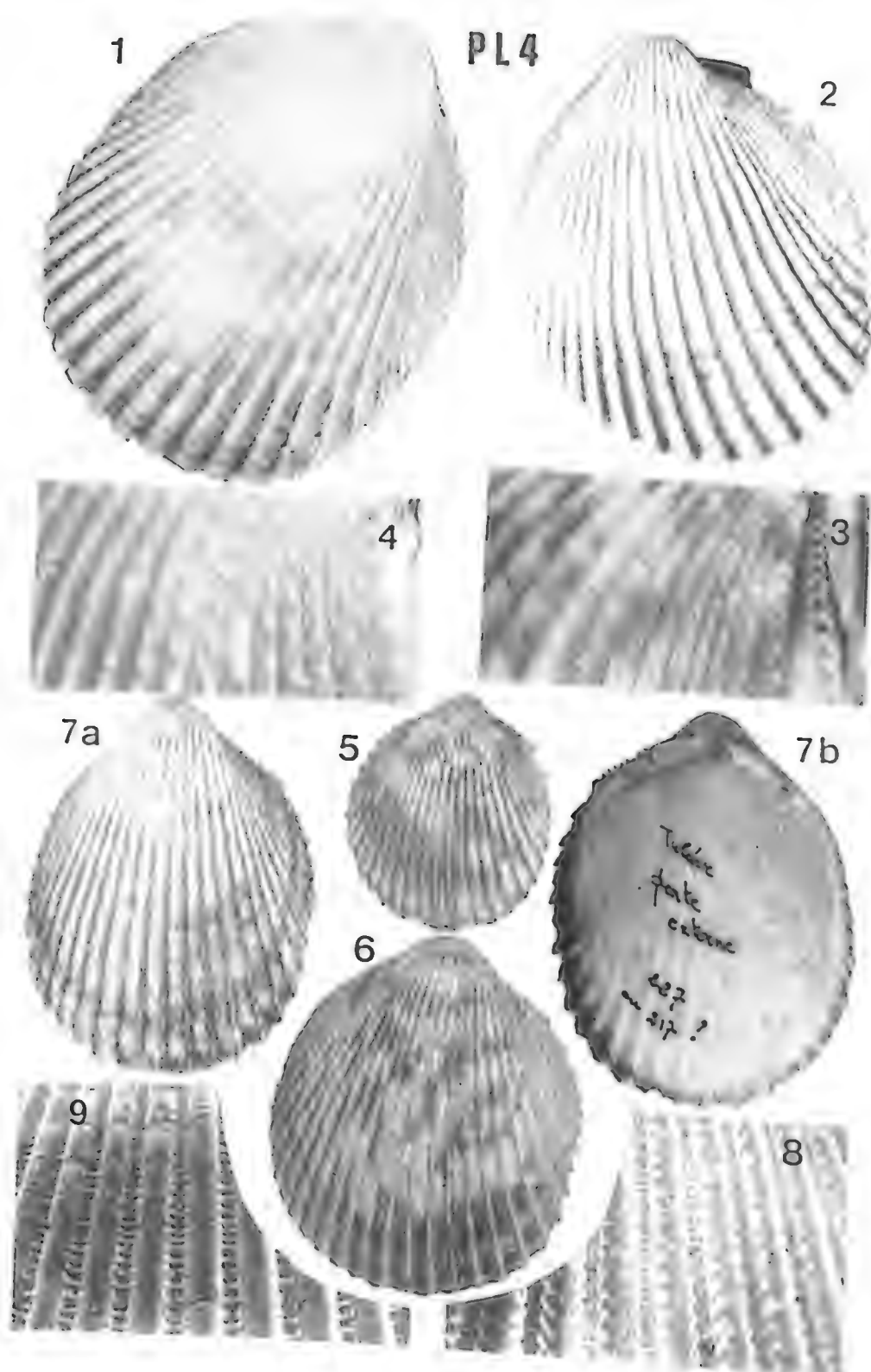
gortanii, from the Pleistocene deposits of the Dahlak Archipelago and Port Sudan. *C. rugosum* is a misidentification of *V. luteomarginatum marerubrum*, as several authors do, but *var. gortanii* has little to do with this species, and represents a valid species, *Vasticardium gortanii* (Nardini, 1937). Many specimens of this species, always Pleistocene fossils, are present in the MNHN, mainly in Plaziat's collection from the southern part of the Gulf of Suez in Egypt, but also from Abulatt Is and Museri Is (Calypso expedition, 1951–52). This fossil species, reaching 100 mm in height, belongs to the "large" *Vasticardium*, but not to the *orbita* group. The most significant differences are that it lacks the characteristic "hooked" anterior laterals and the juvenile rib morphology is closer to *V. elongatum*. Although size, general shape, rib number (range 27–32), are equivalent to those of *V. luteomarginatum*, these two species also differ in several other characters, particularly in the rib morphology of adult PQ and MPQ . As far as I know, this remarkable shell has never been found alive, but being a relatively recent fossil, relict populations could still exist in the Red Sea, or elsewhere.

Vasticardium luteomarginatum insulare subsp. nov.

Pl. 4, figs. 7a–b and 8.

Cardium orbita Reeve (sic) *sensu* Dautzenberg, 1929:382 [Not *Cardium orbita* Broderip & Sowerby, 1833].

Types: Holotype, MNHN, a left valve from Madagascar, Tulear area, Thomassin's diving 1969, sta. 227. Paratype No 1, MNHN, a specimen from Zanzibar, coll. Rousseau. Paratype No 2, MNHN, a right valve from Réunion, coll. Vidal. Paratype No 3, MNHN, a specimen from Mauritius, coll. Carrié. Paratype No 4, AMS C67318, a specimen from Mauritius, coll. Ward.

Diagnosis: Smallest subspecies, never reaching 80 mm in height. Practically equilateral, with rarely a small expansion of posterior part or a slight winging, and generally a very slight curvature of ribs backwards in projection. Never very elongated; moderately depressed (Table 6). External colour beige to yellowish with reddish splashes; MPQ often more coloured. Internal colour white, margin always purple, sometimes purple and yellow. See Table 4 for rib morphology of adult shell.

Plate 4. Figure 1. *Vasticardium luteomarginatum luteomarginatum*. Specimen from Singapore close to Reeve's pl. 13, fig. 47. MNHN. L= 87.6mm. Figure 2. *Vasticardium luteomarginatum marerubrum*: Specimen from Perim labelled by Jousseaume as *Cardium ignotum*. MNHN, coll. Jousseaume. L= 63.6mm. Figure 3. *Vasticardium orbita hawaiiensis*. Specimen from Pearl & Hermes Reef, USNM 428416; detail of the rib sculpture in juvenile PQ, at ligament level. Scale: x 3.5. Figure 4. *Vasticardium luteomarginatum luteomarginatum*. Specimen from the Andaman Sea, MNHN; detail of the rib sculpture in juvenile PQ, at ligament level. Scale: x 3.5. Figure 5. *Vasticardium luteomarginatum luteomarginatum*: Specimen from the Andaman Sea (same as in fig. 4), MNHN coll. Vidal. L= 38.8mm. Figure 6. *Vasticardium luteomarginatum luteomarginatum*. Specimen cited from Swain Reef, Queensland. AMS C303668. L= 56.5mm. Figure 7a–b. Holotype of *Vasticardium luteomarginatum insulare* subsp. nov. MNHN, coll. Thomassin. L= 52.0mm. Figure 8. *Vasticardium luteomarginatum insulare*. Specimen from Ambatoloaka, SW-Nosy Be, Madagascar; detail of the median umbonal sculpture. MNHN, von Cosel coll. Scale: x13.5. Figure 9. *Trachycardium magnum* Linné *sensu* Clench & Smith, 1944. Specimen from Bay of Portobello, Panama; detail of the median umbonal sculpture. MNHN, coll. Vidal. Scale: x25.

Measurements:

	Height (mm)	Length (mm)	Width (mm)	L/H	W/L	Ribs
Holotype [MNHN]	67.2	52.0	(43.0)	0.77	0.83	32
Paratype 1 [MNHN]	70.2	59.7	43.1	0.85	0.72	32
Paratype 2 [MNHN]	63.0	52.1	(43.0)	0.83	0.83	35
Paratype 3 [MNHN]	65.5	53.5	41.5	0.82	0.78	32
Paratype 4 [AMS C67318]	62.0	49.4	39.4	0.80	0.80	34
Zanzibar [MNHN]	80.0	63.2	(48.0)	0.79	0.76	31
Zanzibar [MNHN]	64.9	53.5	(40.0)	0.82	0.75	29
Mauritius [MNHN]	56.8	48.0	35.8	0.85	0.75	34
Seychelles [BMNH,Winwork]	71.2	58.0	44.1	0.81	0.76	33
Doubt. loc. [AMS C14067]	78.6	67.0	48.2	0.85	0.72	32
Other specimen:	49.0	41.9	29.4	0.86	0.70	33

General mean morphometric ratios, shells H over 50.0: 0.82 0.77
     (10 measured in 9 lots) S.D.: 0.026 0.040

General mean rib number (11 counted in 9 lots): 32.6 S.D.: 1.342

Material examined: The type series – Other lots: Seychelles 1(BMNH), 1(IRSNB)– Mauritius 1(LACM), 1(BMNH), 3(AMS), 2(IRSNB)– Madagascar: 2(MNHN)– Kenya: Shimani 1(MNHN)– Zanzibar: 1(MNHN), 1(LACM).

Distribution: Restricted to the southwestern tropical islands of the Indian Ocean, and the East African coast.

Remarks: *V. luteomarginatum insulare* differs from the other two subspecies in its smaller size, purple internal margin, and often by the presence of well developed AT and AOS. It differs from the nominal subspecies by the more pedomorphic rib morphology. *V. luteomarginatum insulare* is, among the three subspecies of *V. luteomarginatum*, the one that most resembles certain medium-sized forms of *V. orbita*, particularly in the subspecies *philippinense*.

Table 6.   Comparison of mean morphometric ratios and rib numbers of subspecies of *Vasticardium luteomarginatum* and *V. orbita*.

| | Vasticardium luteomarginatum | | | | Vasticardium orbita | | |
	marerubrum	insulare	luteomarginatum	philippinense	orbita	mendanaense	hawaiiensis
L/H	0.83	0.82	0.82	0.83	0.78	0.85	0.81
W/L	0.78	0.77	0.78	0.78	0.88	0.82	0.82
Ribs	32.4	32.6	32.7	40.0	45.4	39.4	41.0

Discussion: *Vasticardium orbita and V. luteomarginatum:* species or subspecies?

As discussed, *Vasticardium orbita philippinense* totally disappears to the west of 115°E (Christmas Island excepted) and is replaced by *V. luteomarginatum luteomarginatum*. However, a few specimens of *V. luteomarginatum luteomarginatum* are reported as coming from the east of this line; they are:

1) A specimen labelled from New Caledonia, AMS C14067, old collection, H= 78.6 mm, with 32 ribs, is close to the subspecies *insulare*.

2) A specimen labelled from Ticao, Philippines, de Burgh's collection BM(NH), H= 63.6 mm, with 34 ribs, is identical to forms of *V. luteomarginatum luteomarginatum* from Singapore.

3) A specimen indicated as coming from Swain Reefs, Queensland, AMS C303668, figured by Lamprell & Whitehead (1992: fig. 187) as *Acrosterigma luteomarginata*, H= 65.0 mm with 35

ribs (see pl. 4, fig. 6). This shell, similar to a form of *V. luteomarginatum luteomarginatum*, is the only aberrant record in the Coral Sea, where all other shells of the group, including those from Swain Reef, are *V. orbita philippinense*.

The above three specimens are from old collections, and their presence in an unexpected locality may be due to inadvertent subsequent mixing of lots. Less likely, they could be individual variants of *V. orbita philippinense* with a smaller rib number. The problem is compounded by the stated locality of the holotype of *V. luteomarginatum* being Samar Island, Philippines (with seven specimens in private collections and not seen). This shell is so identical to the Andaman Sea specimens and to some paratypes from Sumatra (zone with AOS and AT only in the medium aged part of the shell, forming a triangle with its apex onwards), that its presence in the Philippines, not previously reported, needs confirmation. According to R. Voskuil (personal communication) this lot originated from a dealer, so an erroneous locality is not impossible.

If the unlikely records are not confirmed, the two species *V. luteomarginatum* and *V. orbita* would be completely allopatric. In view of their many similarities could all forms be considered to be subspecies of *V. orbita*? More observations are needed to solve this problem, but it is considered here to be preferable to separate them at the species level.

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Mineralisation in the teeth of the gastropod mollusc *Nerita atramentosa*

David J. Macey [1]

Lesley R. Brooker [1]

and

Vanessa Cameron [2]

[1] School of Biological and Environmental Sciences, Murdoch University,
Murdoch, WA 6150, Australia

[2] Carmel College, Carmel, WA 6058, Australia

Please address all correspondence to : Dr. D. J. Macey, School of Biological and Environmental Sciences, Murdoch University, Murdoch, WA 6150, Australia.

Abstract

The radula teeth of the littoral gastropod, *Nerita atramentosa,* have been analysed using energy dispersive spectrometry. The matrix of the mature major lateral teeth contains sulfur, chlorine, potassium, calcium and magnesium. The teeth are tanned, and additionally hardened by the possession of biomineralised granules which contain sulfur, chlorine and calcium, together with a large range of other elements including silicon, aluminium, titanium, chromium, iron, nickel, and manganese. These granules, which are incorporated into the matrix of the teeth, result in a surface comparable to sandpaper which presumably serves to increase the abrasive properties of the major laterals. In contrast, the marginal teeth, which are only used for sweeping food particles into the mouth, are not mineralised to the same extent and do not contain granules. This approach to the biomineralisation of their teeth may well have contributed to the competitive success of *N. atrementosa* in the littoral environment.

Introduction

In Australia, as in many other parts of the world, the littoral zone is inhabited by a large variety of molluscs. In many cases these molluscs have specific adaptations which allow them to exploit more fully the environment in which they live. This is particularly the case with regard to feeding, where many species have hardened their teeth using a variety of materials. Such a process, known as biomineralisation, has classically been studied in the patellogastropod limpets and the chitons, though many other mollusc groups also use this technique. In the case of chitons, hardening is via the use of iron whereas both iron and silica are used in patellogastropods (Jones *et al.* 1935, Mann *et al.* 1986, Kim *et al.* 1989, Lowenstam & Weiner 1989, Webb *et al.* 1989). In both of these groups, the biomineralisation process results in teeth in which the organic matrix constitutes a relatively small proportion of the tooth biomass, with the majority of the tooth being infilled with the respective minerals.

Nerita atramentosa Reeve, 1855, is a gastropod mollusc common to the mid-littoral shore region, and whose distribution in Australia stretches from Queensland round the southern coast to the North-west Cape of Western Australia (Wells & Bryce 1986). *N. atramentosa* is a very successful competitor, able to grow faster and live longer than other mollusc species inhabiting the same niche

(Underwood 1978). The genus *Nerita* has a modified rhipidoglossan radula, in that the central rachidian and minor lateral teeth are reduced; the major lateral tooth has a single spoon-shaped cusp as opposed to the classical multi-cusped design; and there is a reduced number of marginal teeth (Hickman 1980). This modification of design presumably enables *Nerita* to scrape surface micro-algae from the rocks on which it lives (Hickman 1980). As such, the diet of *N. atramentosa* consists predominantly of diatoms and algal spores which are possibly replenished with each high tide (Underwood 1978). Though described as a surface film grazer (Underwood 1978), the excavational capabilities of its radula must be substantial, as its faeces are composed of 83% inorganic material (Black *et al.* 1988). In view of the role of biomineralisation in the teeth of chitons and limpets, both of which are known to possess exceptional excavating abilities (Steneck & Watling 1982), this study was initiated in order to determine the degree to which the teeth of *N. atramentosa* are mineralized with elements other than calcium. The possession of such biominerals in this species, which is taxonomically very distinct from the Patellogastropods and Polyplacophora, may well be a contributing factor to its competitive success.

Materials and Methods

Adult specimens of *Nerita atramentosa* (approximately 3 cm in overall shell diameter) were collected from intertidal rock platforms at Rottnest Island, Western Australia (latitude 32° S, longitude 116° E). Following dissection out of the animals, the radulae were cleaned with 5% w/v NaOCl for 10 minutes and fixed overnight using glutaraldehyde (3% by volume) in filtered seawater. For light microscopy samples were examined both prior to and following cleaning. All samples for scanning electron microscopy (SEM) were cleaned and fixed as above, dehydrated through a graded series of alcohols followed by amyl acetate, dried at the critical point of carbon dioxide, mounted on aluminium stubs and coated with either a thin layer of carbon for energy dispersive spectrometry (EDS) or with carbon and gold for photography. In addition, a number of individual lateral and marginal teeth were removed and mechanically damaged to expose a transverse cross section through the tooth core. These teeth were processed as for the whole radulae for SEM observation and EDS analysis. Light microscope measurements were made on a minimum of five animals, and analysis at the electron microscope level on a minimum of three animals. SEM was conducted using a Philips XL20 microscope, while EDS was undertaken using an EDAX 9100 system in the semi-quantitative mode, using both specific area as well as spot analysis for 100 seconds at 15 KeV. This system provides for the semi-quantitative analysis of all elements with an atomic weight greater than that of fluorine. As such, the results for each element are expressed as a relative proportion of all the elements selected for analysis. In order to ensure that a fully representative study was undertaken, specific area analysis was conducted on every fifth row of the radula, at five separate locations, on the major lateral teeth and the inner and outer marginal teeth. In addition, where marked colour changes occurred, every second row was similarly analysed. Spot analyses were conducted when backscattered images indicated the presence of higher atomic weight elements than those normally occurring in the surrounding matrix.

Preliminary analysis revealed the presence of silicon, and in order to further characterise the mineralisation involved, radulae from four animals were dissected out and washed in 0.05M NaOCl for 30 minutes. In order to digest the organic matrix and acid-soluble mineralisation products, the radulae were then incubated in concentrated HCl at 50 °C for 40 minutes, and the remains collected by centrifugation at 16000 g for five minutes (IEC Minimax). The pellet was washed a further five times by resuspension in distilled water, reconcentrated by centrifugation at 16000 g for two minutes, frozen at -80 °C for 10 minutes and then freeze dried overnight. The white fibrous solid that remained after this process was then transferred to a SEM stub coated with carbon impregnated double-sided sticky tape, and viewed under the microscope using both secondary and backscatter detectors. To prevent contamination, all procedures were conducted using plastic utensils and containers.
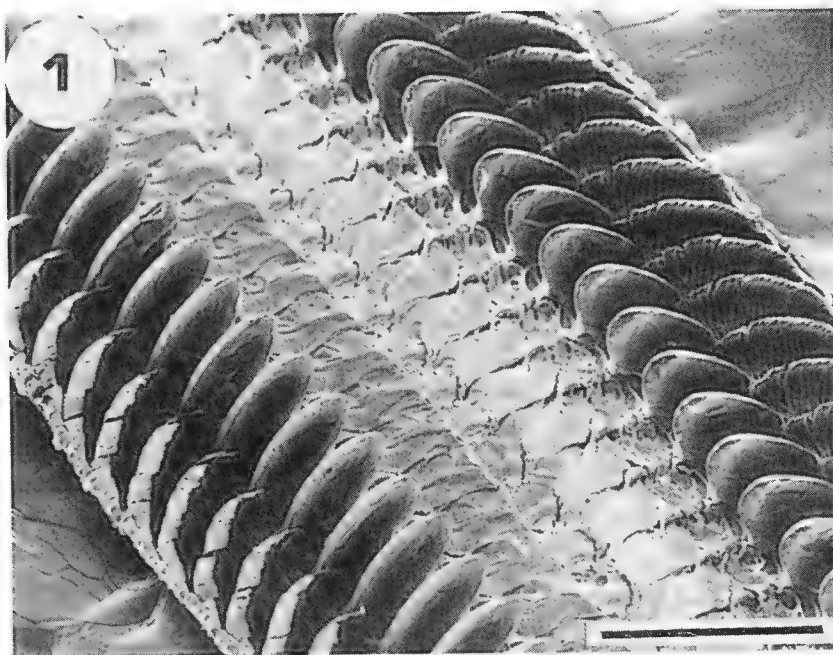
Figure 1.   Scanning electron micrograph (SEM) taken towards the mature end of the radula of *Nerita atramentosa*, showing the enlarged major lateral teeth and the comb-like marginals. Note the major laterals show the presence of a disrupted cuticular layer. Scale bar = 500 µm.

Results

When removed from the animal, the radula of an adult *N. atramentosa* is approximately 26 mm long, 1.6 mm wide and consists of an average of 193 rows of teeth. Each row comprises a small central tooth flanked by a series of relatively flat lateral teeth, followed by the major lateral tooth which has a prominent spade shaped cusp (Fig. 1). On the outer edges of each row are the marginals which consist of a series of fine comb-like teeth (Fig. 1). The radula undergoes progressive maturation down its length, culminating in the teeth that are actually in use. In a freshly dissected radula, the immature major lateral teeth are soft, colourless and transparent in appearance. By approximately row 120, these teeth are yellow in colour, changing progressively to green/black over the next seven rows. From this stage onwards, the teeth are rigid enough to maintain a uniform shape in air. The tips of the inner two thirds of the marginal comb-like teeth exhibit the same colouration as the major laterals. Worn or broken teeth are appreciably lighter in colour. Cleaning in NaOCl results in all coloured teeth changing to a uniform brown. The final ten rows of the radula show progressively increasing patterns of wear towards the mature end, with the last four rows possessing marginal teeth only, the other teeth presumably being lost through wear.

High power examination under the SEM confirmed the picture seen at low magnification, revealing that the major lateral teeth consist of a single cusp with a prominent cutting edge (Fig. 2). In addition, the posterior surface of the non-working mature major lateral teeth exhibit a large number of fine serrations along the cutting edge (Fig. 2), although these are lost as soon as the tooth is used and thus play no functional role in feeding (Hickman 1980). The six most mature teeth show extreme wear. The underlying matrix of the major lateral teeth appears to be covered with a cuticle or surface layer which was presumably disrupted during processing (Fig. 1). A large number of granules, varying in diameter from 0.3 – 1.5 µm, were observed both on the anterior surface close to the cutting edge, and across the whole of the posterior surface of the tooth. These were embedded in
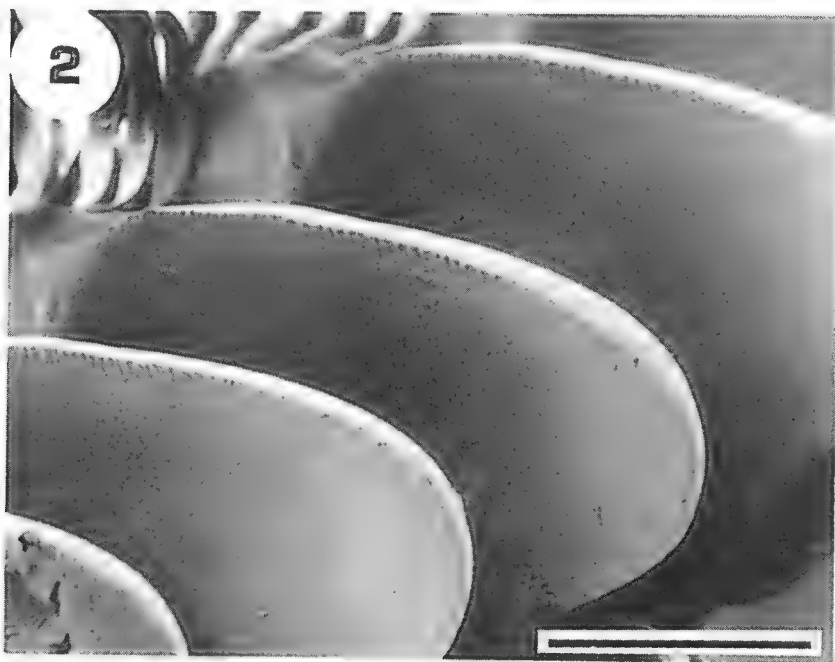
Figure 2.   SEM of unused mature major lateral teeth showing the presence of serrations on the tip. Small granules can
seen on the posterior surface of the teeth. Scale bar = 100 μm.

the tooth matrix, and also associated with the cuticle (Fig. 3). Use of the electron beam to etch away
the outer layers of the posterior surface of unused teeth revealed that the granules were not just
located on the surface of the major lateral teeth, but were embedded deep within the matrix. When
the backscatter detector was utilised, very bright areas were observed, corresponding to the position
of these granules, and indicating that they are composed of material containing elements of higher
atomic weight than those in the surrounding matrix (Fig. 4).

Specific area EDS analysis of the posterior tips of the major lateral teeth at the immature end of
the radula, revealed that chlorine and potassium were the only analysable elements present (Table 1).
Sulfur was first apparent by row 120, and the ratio of sulfur to chlorine reversed with progression
towards the mature end of the radula. Hence, with the exception of row 183 in which the teeth were
clearly worn, from row 150 on, sulfur was the dominant element present. The mature teeth also
contained large amounts of calcium and magnesium, together with aluminium and silicon and small
amounts of phosphorous, potassium and titanium (Table 1). Spot EDS analysis of the mature major

Table 1.   Specific area analysis of the tips of the posterior surface of the major lateral teeth. The composition of each
element is expressed as a weight percent of all elements analysed.

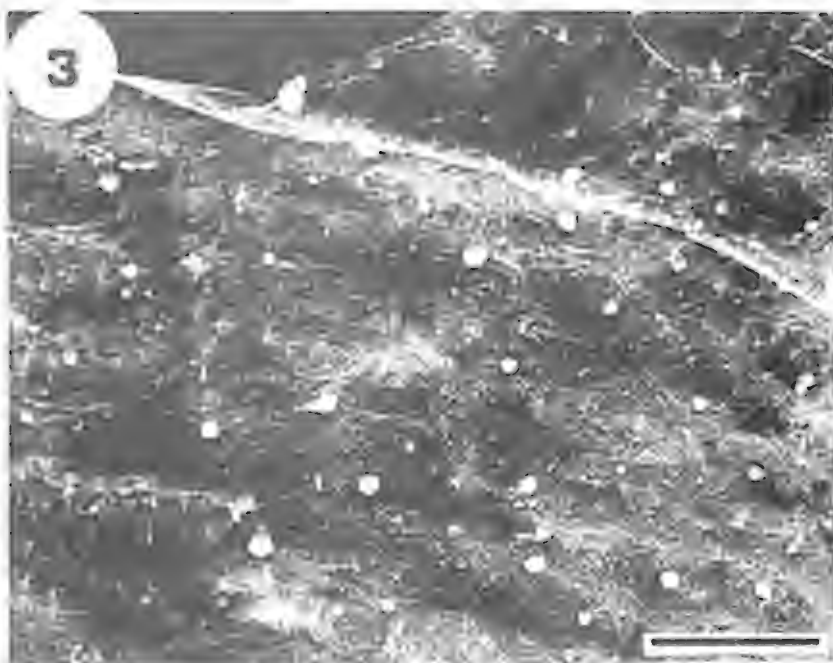|	Mg	Al	Si	P	S	Cl	K	Ca	Ti
Row 100	0	0	0	0	0	66.0	34.0	0	0
Row 120	0	0	0	0	2.7	85.7	11.6	0	0
Row 130	16.9	10.3	9.6	0	18.2	28.0	1.9	14.9	0.2
Row 150	14.4	7.3	6.3	3.2	28.7	21.8	1.7	16.1	0.5
Row 170	12.2	7.3	6.3	3.0	31.9	20.2	1.4	17.6	0.1
Row 183	12.0	8.6	7.9	4.2	28.9	22.2	2.1	13.9	0.2

Figure 3. High power, secondary electron image of the posterior surface of an unused, major lateral tooth showing the presence of granules both on the surface, and embedded in the matrix. Scale bar = 10 µm.
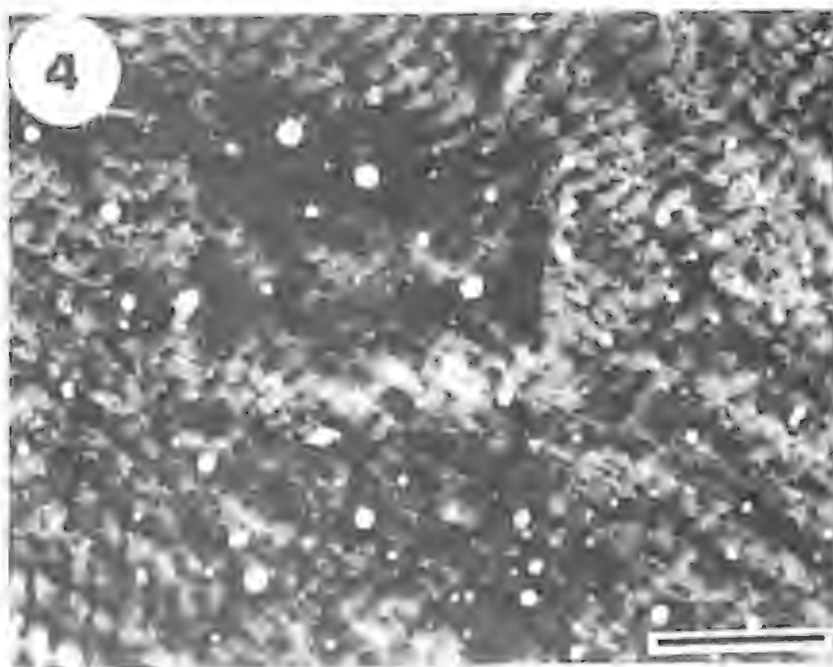

Figure 4. High power, backscattered electron image of the same region as in Figure 3, showing bright areas corresponding to the position of the granules, and which are indicative of the presence of higher atomic weight elements. Scale bar = 10 µm.

Table 2.   Specific area analysis of inner and outer marginal (comb) teeth at row 170. The composition of each element is expressed as a weight percent of all elements analysed.

	Mg	Al	Si	P	S	Cl	K	Ca	Ti
Inner	10.3	4.9	3.7	1.6	22.6	39.2	2.4	15.2	0.1
Outer	8.8	4.8	3.0	4.8	11.2	42.6	4.6	20.2	0.2

lateral teeth, conducted away from the granules, revealed only the presence of sulfur, chlorine, potassium, calcium and magnesium. However, when the granules themselves were similarly analysed, a different picture emerged. Thus, while neither magnesium nor potassium were detected, in addition to sulfur, chlorine and calcium, a large range of other elements was found including silicon, aluminium, titanium, chromium, iron, nickel, and manganese, with the exact composition depending on the specific granule analysed.

The marginal teeth resemble a comb in structure consisting of approximately 35 individual teeth. The inner 25 possess smooth tips, while the outer 10 exhibit a serrated margin. Additional marginal teeth at the edge of the radula are reduced in size and fused together. Specific area analysis of all immature marginal teeth revealed that they contained chlorine and potassium, with calcium first being detected by row 100. The mature inner marginal teeth, corresponding to the coloured marginals seen under the light microscope, contained chlorine, sulfur, calcium and magnesium, together with aluminium and silicon, and small amounts of phosphorous, potassium and titanium (Table 2). The colourless, mature, outer marginal teeth contained the same elements with the major difference in composition being that they possessed considerably less sulfur (Table 2). No apparent difference in composition was found between different rows of mature marginal teeth down the length of the radula.

When mechanically fractured major lateral teeth were viewed using both the secondary and backscattered detectors, no compositional differences were detected between their inner and outer regions. Similarly fractured marginal teeth appeared relatively homogeneous throughout, with no granules observed in either intact or broken marginal teeth and no bright spots seen using the backscattered detector.

Acid digestion of the teeth resulted in a white particulate material with a fibrous appearance. Examination using SEM revealed that it was composed of a large number of highly reflective particles with a size range of 0.2 – 1.0 µm, similar to that of the granules embedded in the mature major lateral teeth. EDS analysis of these particles revealed that a large number contained appreciable amounts of silicon, aluminium and titanium. However, as occurred when individual granules were analysed, a large variety of other elements was detected, with their relative proportions depending on the particle selected for analysis.

Discussion

The results detailed in this study have shown for the first time that the major lateral teeth of *Nerita atramentosa* incorporate small calcified granules which differ, both in structure and elemental composition, from the overall tooth matrix. The distribution of these granules, restricted as they are to the matrix of the anterior tip and posterior side of the major laterals, which are the main scraping teeth, suggests that they are involved in increasing the abrasive properties of the tooth as a whole. Indeed, as has been suggested for patellogastropod limpets (Vincent 1980), our studies have shown that once the teeth are in use, the matrix is preferentially worn away to expose the granules, giving a surface comparable to sandpaper. The presence of considerable quantities of magnesium in the tooth matrix, compared to its total absence in the granules, implies that its exclusion imparts very different structural properties to these granules. A similar situation has been described for the Perciform fishes

where magnesium, present in the bulk of the tooth, is conspicuously absent from the cutting edge, which is described as being much harder (Suga *et al.* 1992). The presence, following acid-digestion, of a residue composed of particulates, similar in size to the tooth granules, suggests that some of the minerals which occur in the granules differ in their chemical nature from those which are found in the matrix of the tooth. In the teeth of limpets, it has been suggested that silicon may be bound within the organic matrix prior to the impregnation of amorphous silica (Mann *et al.* 1986). The continued presence of silicon and aluminium in the acid-digested particles is indicative that these elements may be present in the granules in the form of amorphous silica and/or aluminosilicates. Although the benefit of the sandpaper approach to biomineralisation in individual teeth may be short-lived, this is compensated for by the radula in many molluscs, including *Nerita*, having a relatively rapid rate of tooth turnover (Runham 1962, Fretter 1965).

In *N. atramentosa,* the radula is composed of variously shaped teeth with specialised roles and mechanical properties. As in other neritids, the major lateral teeth are considerably enlarged and serve as the main scraping implements (Baker 1923, Fretter 1965), with the working teeth exhibiting extreme wear and being lost prior to adjacent teeth of the same row. Throughout the radula, the increasing colour observed at the light microscope level corresponds to a relative increase in the amount of sulfur. The presence of sulfhydryl groups has been associated with tanning, both in the radulas of other molluscs, and in arthropod cuticle (Runham 1963, Wigglesworth 1972). Hence, it is assumed that the presence of colour is indicative of cross-linking of the constituents of the radula matrix. Additional hardening of these teeth is achieved by the incorporation of biomineralised granules. The less robust marginal teeth exhibit little wear, and are only responsible for sweeping food into the mouth as the radula is retracted (Fretter 1965, Steneck & Watling 1982). The inner mature marginals are coloured (and presumably tanned), and mineralised to a level comparable to that which occurs relatively early in the development of the major lateral teeth. The serrated outer marginal teeth only contain half the amount of sulfur found in the inner marginals, and are not mineralised to the same extent, presumably reflecting their roles in particle size selection of food and as accessory sweepers (Hickman 1980). Despite the marginal teeth possessing the same range of elements as the major laterals, no granules were observed in either intact or broken marginal teeth and no bright spots could be seen using the backscatter detector. This observation lends further support to the suggestion that there is a link between the presence of the granules themselves, and the abrasive function of the major lateral teeth.

The presence of granules of a similar size to those recorded in this study, and also containing a variety of elements including heavy metals, is well documented in invertebrates, where they have a role in detoxification processes (see *e.g.* Taylor & Simkiss 1984). Indeed, this may have been their original purpose in *N. atramentosa,* as they would rapidly be removed from the body through radula tooth turnover (Runham 1962). The need for such a mechanism may have arisen as a result of the diatom rich diet of *N. atramentosa* (Underwood 1978). Diatom frustules are primarily composed of silica, with other elements such as aluminium, iron and titanium naturally bound to the surface (Werner 1977). Hence the ingestion of diatoms could account for the presence of these elements in the tooth granules. Aluminium and silicon have also been reported as occurring in the rectal gland granules of the sea urchin *Echinocardium* (Brown 1982). However, if the granules in *N. atramentosa* originally played a primary excretory role, some modification in their composition must have occurred, as magnesium, which is a relatively common component of excretory granules, is present in the tooth matrix, yet is absent from the granules.

The incorporation of hardening minerals into the teeth of animals has been known to take a variety of forms. For example, in chitons and limpets the mineral products occupy a discrete architectural compartment within the overall tooth structure (Mann *et al.* 1986, Kim *et al.* 1989, Lowenstam & Weiner 1989). In rats and tetra-odontiform fishes, the minerals are incorporated as part of the matrix structure (Selvig & Halse 1975, Suga *et al.* 1989), while in spiders and chaetodontid fishes they form a cuticular layer covering the core (Schofield & Lefrevre 1989, Sparks *et al.* 1990). All three approaches enable the exploitation of a resource that would otherwise prove difficult, or indeed

impossible to use. In Western Australia, *N. atramentosa* occupies the same niche as the chiton *A. hirtosa,* with which comparisons can be made. Both species possess a similar radula design, in that the major lateral teeth are enlarged and have a reduced number of contact points with the substratum. In addition, both species have employed biomineralisation over and above the simple deposition of calcium carbonate, to enable them to browse the hard substrate on which they subsist. The excavating abilities of their respective radulae is demonstrated by the faeces of both species containing between 80 and 90% inorganic material (Black *et al.* 1988, Macey *et al.* 1996), though a proportion of this may result from the acquisition of material previously loosened by filamentous and boring algae (Ginsburg 1953, Lowenstam 1962, Raffaelli 1985). The success of *N. atramentosa* has been attributed to its fast rate of movement and rapid feeding (Underwood 1978). While the latter could be partially attributed to the size of the radula teeth (Black *et al.* 1988), the increased tooth hardness, through the possession of mineralised granules, may also play a significant role.

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Spatial and temporal patterns of abundance and the effects of disturbance on under-boulder chitons

K. A. Smith

School of Biological Science
University of New South Wales
Kensington, New South Wales 2052
email: 8941912@unsw.edu.au

and

N. M. Otway

Fisheries Research Institute
P. O. Box 21
Cronulla, New South Wales 2230

Abstract

The spatial and temporal patterns of abundance of 8 species of chiton found under boulders were documented at sites in the mid- and low-shore regions of an extensive boulder-field in the Long Reef Aquatic Reserve. The mean number of species and mean densities of *Ischnochiton australis* (Sowerby, 1840), *Ischnochiton elongatus* (Blainville, 1825), *Ischnochiton versicolor* (Sowerby, 1840), *Cryptoplax mystica* (Iredale & Hull, 1925), *Callistochiton antiquus* (Reeve, 1847), *Ischnochiton smaragdinus* (Angus, 1894) and *Acanthochiton* spp. did not vary through time during the 6 month study, conducted over the autumn and winter months. However, their abundances varied at small (areas 3 m apart) and large (sites 60 m apart) spatial scales in the mid- and low-shore regions. Abundances ranged between 0 and 28 individuals 1000 cm^{-2} of boulder surface over the study period.

Relationships between the abundances, sizes and numbers of species and the size of the boulder and/or the underlying sediments were rare, contrasting with suggestions made in early taxonomic studies. However, the sizes of *I. australis* in the low-shore and *I. elongatus* in the mid-shore were positively correlated with boulder size and the density of *I. elongatus* was positively correlated with the proportion of fine grained sediment.

A manipulative field experiment was done to examine possible sampling-induced changes in abundances. The mean number of species, total number of individuals and mean densities of *Ischnochiton australis*, *Ischnochiton elongatus*, *Ischnochiton versicolor* all declined following the overturning of boulders. The experiment also showed that despite the alterations to the habitat caused by our sampling, the abundances of the under-boulder chitons were not significantly altered. Therefore our data documenting patterns of abundance in space and time were not confounded by sampling-induced disturbance.

Introduction

Chitons have a worldwide distribution and are particularly abundant and speciose on the west coasts of North and South America and in Australasia (Dall 1919, Iredale and Hull 1927, Otaiza and Santelices 1985). Recent studies (*e.g.* Paine 1984, Duggins and Dethier 1985) have suggested that chitons play a major role in structuring the low-shore algal communities on rocky shores. In contrast,

little, if anything, is known about the ecology of chitons inhabiting boulder communities. The information that is available is restricted to about 20 species and concerns their taxonomy (Smith 1960), abundances and diets (Andrus and Legard 1975, Fulton 1975) and reproduction (Creese 1986). Chitons are often the most prevalent of the molluscan grazers found under boulders (Morton and Miller 1968, McGuinness 1984). It is not known at this stage whether they have any demonstrable effects on the other organisms comprising this community. In addition to possible effects on the abundances of algae, chitons could affect the densities of sessile organisms through the "bulldozing" (*sensu* Dayton 1971) and/or inadvertent consumption of new recruits.

Boulder communities are useful sites in which to study the development and maintenance of marine benthic communities. Research in these habitats (*e.g.* Osman 1977, Leiberman *et al.* 1979, Sousa 1979, McGuinness 1987a, b) has examined concepts of community stability, species-area relationships, successional changes and the effects of physical disturbance on community structure. A diverse group of organisms including ephemeral and perennial algae (Sousa 1979, Leiberman *et al.* 1979), and sessile (*e.g.* barnacles, tubeworms, sponges and ascidians) and mobile (*e.g.* polychaetes, limpets, periwinkles and chitons) animals (Pope 1943, McGuinness 1987a, b) make up these communities. Boulder communities are also important habitats for the recruitment of sea urchins (Tegner and Dayton 1977, 1981) and abalone (Shepherd 1973, Sainsbury 1982), animals that are important as marine herbivores and as seafood.

The ecology of chitons in Australia is poorly studied. Apart from taxonomic studies (*e.g.* Allan 1950, MacPherson and Gabriel 1962), there are a few studies which deal with aspects of reproduction (Turner 1978, Sakker 1986, Wells and Sellers 1987) and only a handful of studies on the distribution and abundance, diets, movement and effects of grazing (Thorne 1967, Otway 1989, 1994). This situation is made worse when one considers that a large proportion of Australian chitons are found under boulders and that the present ecological information concerning this habitat is restricted to three studies, those of Pope (1943), Kangas and Shepherd (1984) and Currie (1990). Consequently, much of the information concerning the distribution and abundance of under-boulder chitons in Australia must be inferred from the descriptive and taxonomic accounts (Pope 1943, Allan 1950, MacPherson and Gabriel 1962, Dakin 1952). These suggest that distribution and abundance are influenced by factors such as boulder size, sediment type and height on the shore.

Given the paucity of information concerning under-boulder chitons in SE Australia, our study was designed to examine three principal areas of interest. First, we considered it important to test the prior assertions of Dakin (1952) who inferred relationships between the distribution and abundance of under-boulder chitons and boulder size, sediment type and height on the shore. Second, we documented the spatial and temporal patterns of abundance of under-boulder chitons. Third, we used a manipulative field experiment to examine the effects of sampling-induced disturbance on the abundances of under-boulder chitons.

Materials and methods

This study was done at Long Reef Aquatic Reserve, Collaroy, N.S.W. (33°45'S, 151°19'E). The headland of Long Reef is surrounded by an extensive rock platform interspersed with small, sandy beaches and boulder zones. The platform, boulders and surrounding cliff faces consist of Collaroy Claystone ("chocolate shale") of the Narrabeen Group (McElroy, 1969). The study was done in the boulder field adjacent to Collaroy Beach, on the northern side of the headland, and is partially protected from the dominant south-easterly swell. Sampling was done during low water and boulders were collected from areas located 0.0 to 0.5 m above Mean Low Water Springs (chart datum for Sydney). The under-boulder community here is similar to that of other boulder fields along the N.S.W. coast (Dakin 1952, McGuinness 1987a, b).

Boulder Size

The surface area of the underside of each boulder was estimated by measuring appropriate

dimensions of the boulder. For example, the base and perpendicular height were measured if it was triangular or the diameter if it was approximately circular. The surface areas were then calculated using appropriate geometrical formulae. The areas of a random subsample of boulders were also calculated by tracing the boulder shape on plastic sheeting, a method considered more accurate than the use of geometrical formulae. Comparison of the two methods found the geometrical formulae overestimated the area of boulders by 6 percent, on average, but their use was favoured because the tracing of all boulders sampled could not completed within the time available.

Sediment

Sediment samples were collected after recording the abundances of each chiton species under boulders. At least 30 ml of sediment was collected from under 78 boulders in the low-shore and mid-shore regions. Samples were then dried to constant weight and sieved into 3 fractions. These fractions were fine sand (< 0.425 mm), coarse sand (> 0.425 mm to 1.400 mm) and gravel and shell grit (> 1.400 mm to 3.360 mm). The proportion of each fraction in each sediment sample was determined by weight measured to the nearest 1 mg.

Size of chitons

The size of chitons has been documented by measuring the anterior-posterior lengths of individuals in the field (*e.g.* Glynn 1970, Baxter and Jones 1978). Such measurements can lead to substantial errors because of the curvature of the substratum (a boulder in this study) underlying any given individual. To avoid this source of error we recorded the width of the fourth shell-plate, or the first shell-plate of *Cryptoplax mystica*, as these measurements are linearly related to the maximum length of the chiton and are not affected by the curvature of the substratum underlying the chiton (Wells and Sellers 1987, Otway 1994 and see Results). The width of the appropriate shell-plate was measured to the nearest 0.1 mm using dial calipers. However, individuals of *Acanthochiton granostriatus* (Pilsbry, 1894) and *A. retrojectus* (Pilsbry, 1894) were not measured because of their small size and because the two species could not be distinguished in the field.

Sampling of chitons

Boulders were overturned and the number of chitons of each species found on the underside of each boulder was recorded. Any chitons that fell from the boulder during overturning were collected, identified and measured before being returned to the base of the boulder when sampling was complete. After sampling, each boulder was returned to its original position and orientation. The densities of all chitons were scaled to the number of individuals 1000 cm^{-2} prior to analysis.

The spatial and temporal patterns in the abundances of under-boulder chitons were documented at four sites: 2 in the mid-shore and 2 in the low-shore regions of the boulder zone. No sampling was done in the high-shore regions because a preliminary survey (Smith 1992) had shown that no chitons were found under boulders in this region. Sampling was done from March to August, 1992. Each month, 20 randomly chosen boulders were sampled from each of 2 replicate areas (3 x 3 m) randomly located in each of 4 sites (10 x 10 m). Areas within Sites were at least 3 m apart and Sites at the same height on the shore were separated by approximately 60 m. Each month, new areas were selected at random from within each site to minimize sampling of boulders disturbed by prior sampling. On each occasion, 160 boulders were sampled; 80 from each of the mid- and low-shore regions. It is possible, however, that some boulders were sampled more than once during the 6 months of sampling.

Effects of sampling-induced disturbance

A manipulative field experiment was set up to examine the effects of disturbance on the abundances of under-boulder chitons. We were particularly concerned with changes that may occur following our sampling of the boulders as this could confound our studies of the spatial and temporal patterns of

abundance. The experiment consisted of 3 treatments: an undisturbed control in which the boulders were sampled and then removed from the site, together with any chitons attached to these boulders, to ensure that they were not sampled again (C); a treatment which followed our normal sampling protocol (D) and a treatment in which boulders were sampled and then replaced in an overturned position (O). Boulders in the latter two treatments (D and O) were marked with numbered tags to permit subsequent identification and sampling of the same boulders. During the tagging process, care was taken not to damage or destroy any animals. Those chitons that attempted to crawl away or fell off the rock during tagging were recaptured and placed at the base of the rock when it was returned to the boulder field. The experiment was done during August, 1992 and replicated at 3 sites in the low-shore region. At each site, 18 boulders of similar size were selected at random. Six boulders were then assigned, at random, to each treatment. One month later, the boulders in treatments D and O, plus six undisturbed boulders (selected at random) were again sampled at each site after 1 month to match the sampling interval adopted to document the patterns of abundance.

Analysis of Data

Possible correlations between the densities of chitons and grain size were examined using Pearsons partial correlation analysis. Relationships between the sizes and abundances of chitons and the size of boulders were also examined.

Data concerning the spatial and temporal patterns of under-boulder chitons were analysed using a partially orthogonal, partially nested, four factor analyses of variance with Times – random, Heights – fixed, Areas nested within Heights – random and Sites nested within Months, Heights and Areas – random. Note that this does not permit a test of Heights main effects term, but this is not crucial as the factor Heights was addressed in interaction terms.

The effects of disturbance were assessed by fully orthogonal three factor analyses of variance with Times (Before vs. After) – fixed, Sites – random and Treatments – fixed. To ensure the temporal independence of replicates within each treatment, 3 replicate boulders were chosen at random from the 6 in each treatment at each site to provide the "before disturbance" data. The remaining replicates in the disturbed and overturned treatments provided the "after disturbance" data. Data from 3 boulders (selected at random) from the 6 undisturbed (control) boulders sampled after 1 month (as described in subsection "Effects of sampling-induced disturbance") also provided "after disturbance" data. This procedure has the potential to reduce the power of the tests for treatment effects. Where possible post-hoc pooling of terms in the original model was done to provide more powerful tests of the remaining sources of variation (see Winer 1971 and Results).

Preliminary tests for homogeneity of variances were done prior to analysis of variance using Cochran's test (Snedecor and Cochran 1980). When necessary, data were transformed following standard procedures (for details see Winer 1971, Underwood 1981a). Post-hoc identification of significant differences among means was done using Student-Newman Keuls (SNK) tests (Winer 1971, Snedecor and Cochran 1980).

Results

Correlations with boulder size

Neither the number of species nor the total number of individuals was correlated with boulder size. The number of individuals of *Ischnochiton australis, Ischnochiton elongatus, Ischnochiton versicolor, Cryptoplax mystica, Callistochiton antiquus* and *Ischnochiton smaragdinus* also showed no correlations with boulder size.

The widths of the fourth shell-plate of *I. australis, I. elongatus, I. versicolor, I. smaragdinus* and *C. antiquus* were all linearly related to their anterior-posterior lengths and each regression of length on width accounted for at least 90% of the variation in their lengths (Table 1). The width of the first shell-plate of *C. mystica* was linearly related to the anterior-posterior length and the regression of

Table 1. Regression and correlation analyses for under-boulder chitons at Long Reef. [1] Regressions of the length of the individual on the width first shellplate for *Cryptoplax mystica* and the width of the fourth shell-plate for *Ischnochiton australis*, *Ischnochiton elongatus*, *Ischnochiton versicolor*, *Callistochiton antiquus* and *Ischnochiton smaragdinus*. [2] Correlation coefficients calculated using n=78, partial correlation coefficients calculated using n=75. *, **: significant at $p < 0.05$ and $p < 0.01$ respectively; – : insufficient data.

| Species | Maximum shell width | Regression of body length on shell width [1] | | Correlation coefficients of boulder size and chiton size in low- and mid-shore regions | | Correlation coefficients of chiton abundance and proportion of sediment fractions (partial coefficients given in brackets) [2] | | |
		Regression Equation	r^2	Low-Shore	Mid-Shore	fine	coarse	gravel
I. australis		y = -2.219+2.244x (n= 70)	0.901	0.328** (n=98)	0.279 (n=22)	0.250* (-0.083)	-0.281* (-0.139)	-0.073
I. elongatus		y = -0.550+3.00lx (n=68)	0.916	0.071 (n=20)	0.694* (n=12)	0.406** (0.339**)	-0.369** (-0.283*)	-0.279* (-0.277*)
I. versicolor		y = -0.743+2.822x (n=16)	0.925	0.863 (n=4)	-	-	-	-
C. mystica		y = -3.699+10.966x (n=31)	0.602	0.217 (n=35)	0.089 (n=21)	0:112	-0.104	-0.075
C. antiquus		y = -2.069+2.899x (n=41)	0.927	0.118 (n=22)	0.462 (n=9)	0.190	-0.214	-0.054
I. smaragdinus		y = -1.326+2.365x (n=18)	0.931	0.381 (n=4)	-	-	-	-

length on width accounted for 60% of the variation in length. Of these, *I. australis* and *I. elongatus* were the largest of the abundant species. In most cases the size of individuals of each species showed no significant correlation with boulder size, however, the sizes of *I. australis* in the low-shore and *I. elongatus* in the mid-shore were positively correlated with boulder size.

Correlations with sediment

Chiton densities were correlated with the proportion of each sediment fraction (Table 1). The abundances of 2 species were significantly related to grain size ($p < 0.05$). The density of *I. elongatus* was positively correlated with the proportion of fine sand (r = 0.406), and negatively correlated with the proportions of coarse sand (r = -0.369) and gravel (r = -0.279). The density of *I. australis* was also positively correlated with the proportion of fine sand (r = 0.250) and negatively correlated with the proportion of coarse sand (r = -0.281), but not significantly correlated with the proportion of gravel (r = -0.073).

The densities of *I. elongatus* and *I. australis* were also significantly positively correlated with each other (r = 0.449). Therefore partial correlations were performed to eliminate any effect of one species on the other (Table 1). Eliminating the effect of *I. australis* did not alter the significance of the correlations of *I. elongatus* density with any sediment fraction (fine r = 0.339, coarse r = -0.283, gravel r = -0.277). However, by eliminating the effect of *I. elongatus*, the correlations of *I. australis* density with each sediment fraction were no longer significant (fine r = -0.083, coarse r = -0.139).

Spatial and temporal patterns of abundance

The number of species and total number of individuals occurring under boulders (Fig. 1) did not exhibit significant temporal variation between Sites nested within Heights on the shore (Table 2,
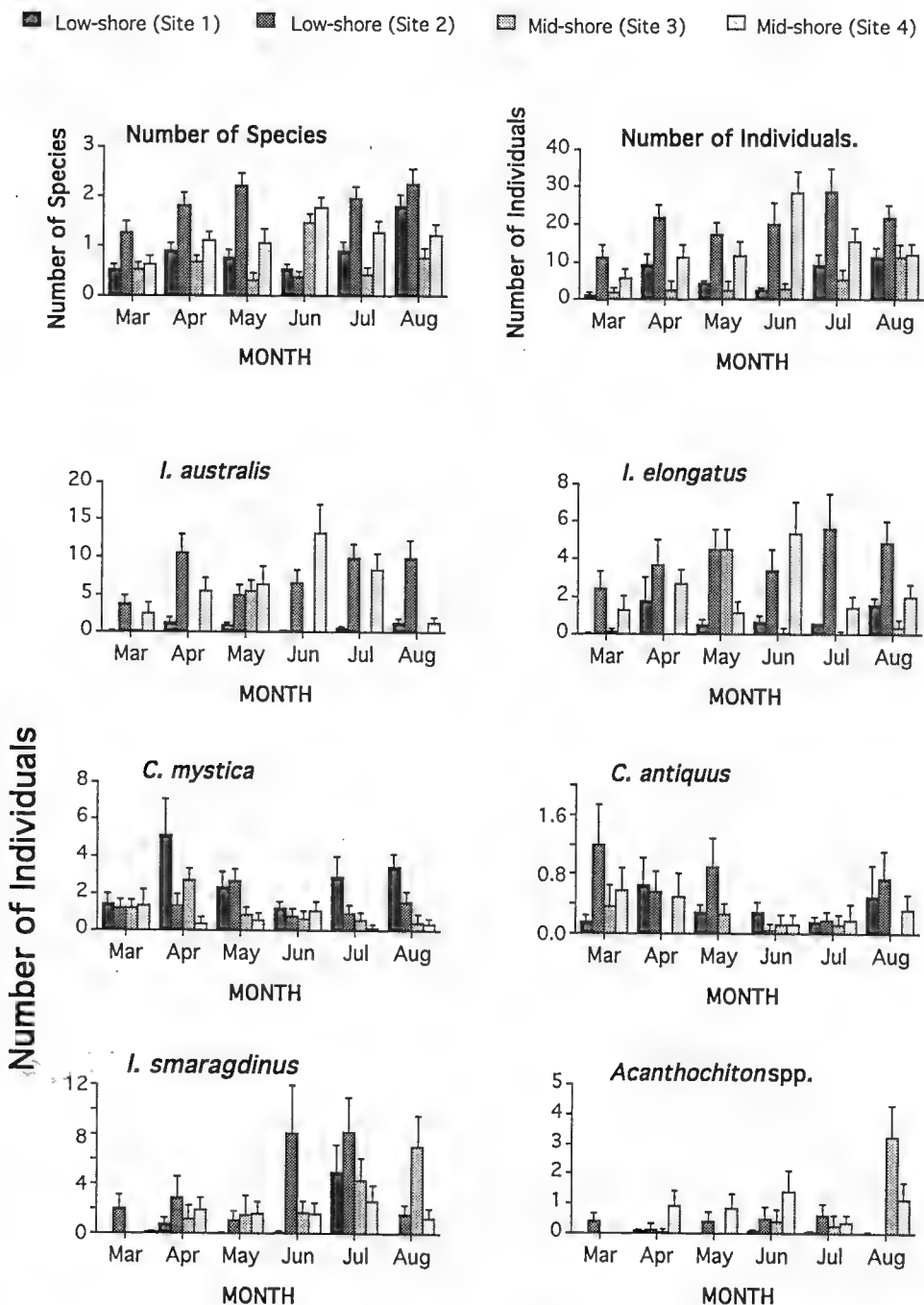
Figure 1.   Mean (± SE) number of species, total number of individuals, and the numbers of *Ischnochiton australis*, *Ischnochiton elongatus*, *Cryptoplax mystica*, *Callistochiton antiquus*, *Ischnochiton smaragdinus* and *Acanthochiton* spp. found under boulders at replicate sites in the mid- and low-shore regions at Long Reef from March to August, 1993.

Table 2. Analyses of variance of the number of species, total number of individuals, and the numbers of *Ischnochiton australis, Ischnochiton elongatus, Ischnochiton versicolor, Cryptoplax mystica, Callistochiton antiquus, Ischnochiton smaragdinus* and *Acanthochiton* sp. found under boulders in the mid and low-shore regions at Long Reef from March to August, 1993. df: degrees of freedom; MS: mean square; *,** significant at p<0.05 and *p*<0.01 respectively; NS: not significant at *p*>0.05; -: no appropriate mean square denominator for F ratio.

Source of variation	(df)	Number of species		Number of chiton individuals		I. australis		I. elongatus		I. versicolor	
		MS	F	MS	F	MS	F	MS	F	MS	F
Times	5	10.64	*	3.33	NS	0.113	NS	0.092	NS	0.341	NS
Height	1	73.7	-	7.48	-	0.756	-	0.527	-	1.683	-
Sites(Heights)	2	77.85	**	21.35	**	0.554	**	1.052	**	1.941	**
Areas(Sites(Height(Times)))	24	5.63	**	1.35	**	0.127	**	0.068	**	0.136	**
Times x Heights	5	6.4	NS	0.79	NS	0.128	NS	0.078	NS	0.141	NS
Times x Sites(Heights)	10	2.96	NS	1.06	NS	0.092	NS	0.029	NS	0.151	NS
Residual	912	1.08		0.29		0.025		0.020		0.043	
Total	959										

Source of variation	(df)	C. mystica		C. antiquus		I. smaragdinus		Acanthochiton	
		MS	F	MS	F	MS	F	MS	F
Times	5	0.046	NS	0.041	NS	424.85	NS	0.113	NS
Height	1	0.812	-	0.008	-	54.15	-	0.452	-
Sites(Heights)	2	0.087	NS	0.028	NS	511.64	*	0.109	NS
Areas(Sites(Height(Times)))	24	0.065	**	0.008	NS	84.09	NS	0.069	**
Times x Heights	5	0.076	NS	0.011	NS	191.18	NS	0.215	NS
Times x Sites(Heights)	10	0.037	NS	0.016	NS	142.41	NS	0.107	NS
Residual	912	0.018		0.008		74.05		0.036	
Total	959								

analyses of variance, $p > 0.05$). However, both the number of species and total number of chitons differed significantly at the two spatial scales of Sites (60 m apart) and Areas within Sites (3 m apart) (Table 2, analyses of variance, $p < 0.001$). Small-scale differences in the number of species and total number of individuals occurred between Areas in the mid-and low-shore regions (Table 3, SNK tests, $p = 0.05$). At the larger spatial scale, there were significantly more species under boulders at Site 3 in the mid-shore and Site 2 in the low-shore (Table 2, SNK tests, $p = 0.05$). The number of

Table 3. Summary of results of SNK tests showing the months in which abundances of chitons in areas nested within sites were significantly different in the mid- and low-shore regions at Long Reef. (- denotes no significant differences)

Variable	Mid-shore		Low-shore	
	Site 3	Site 4	Site 1	Site 2
Number of species	-	Mar, May, Aug	Apr	Apr
Number of Individuals	-	Mar, May, Jun, Aug	Apr	May
I. australis	-	Mar, Apr, May, Jun, Jul	May	Apr, May
I. elongatus	-	-	-	Mar, Apr, May, Jun, Aug
I. versicolor	-	Aug	-	Apr, Jul
C. mystica	-	Jun	Mar, Apr, Aug	Mar, Apr
Acanthochiton spp.	-	May, Jun, Aug	-	-

individuals only differed between sites in the low-shore with significantly more individuals occurring at Site 2.

The densities of *Ischnochiton australis*, *Ischnochiton elongatus* and *Ischnochiton versicolor* (Fig. 1) did not vary through time at Sites nested within Heights on the shore, but all three species differed at the large and small spatial scales (Table 2, analyses of variance, $p > 0.05$ and $p < 0.01$, respectively). Densities of *I. australis* and *I. versicolor* differed between areas in the mid- and low-shore regions with *I. versicolor* only differing on three occasions (Table 3, SNK tests, $p = 0.05$). However, densities of *I. elongatus* only differed between areas in the low-shore region (Table 3, SNK tests, $p = 0.05$). At the larger spatial scale, *I. australis* and *I. elongatus* had significantly greater densities at Site 2 in the low-shore and at Site 4 in the mid-shore (Table 2, SNK tests, $p = 0.05$). *I. versicolor* on the other hand only differed in the low-shore with significantly greater densities occurring at Site 1 (Table 2, SNK tests, $p = 0.05$).

The densities of *Ischnochiton smaragdinus* and *Callistochiton antiquus* (Fig. 1) did not fluctuate through time at Sites nested within Heights on the shore, but there were significant differences in space (Table 2, analyses of variance, $p > 0.05$ and $p < 0.01$, respectively). Neither *I. smaragdinus* nor *C. antiquus* differed in density between Areas, but both species exhibited significant differences at the larger scale of Sites (Table 2, analyses of variance, $p > 0.05$ and $p < 0.01$, respectively). *I. smaragdinus* had significantly greater densities at Site 2 in the low-shore and did not differ between sites in the mid-shore (Table 2, SNK tests, $p = 0.05$). *C. antiquus* exhibited the opposite pattern and

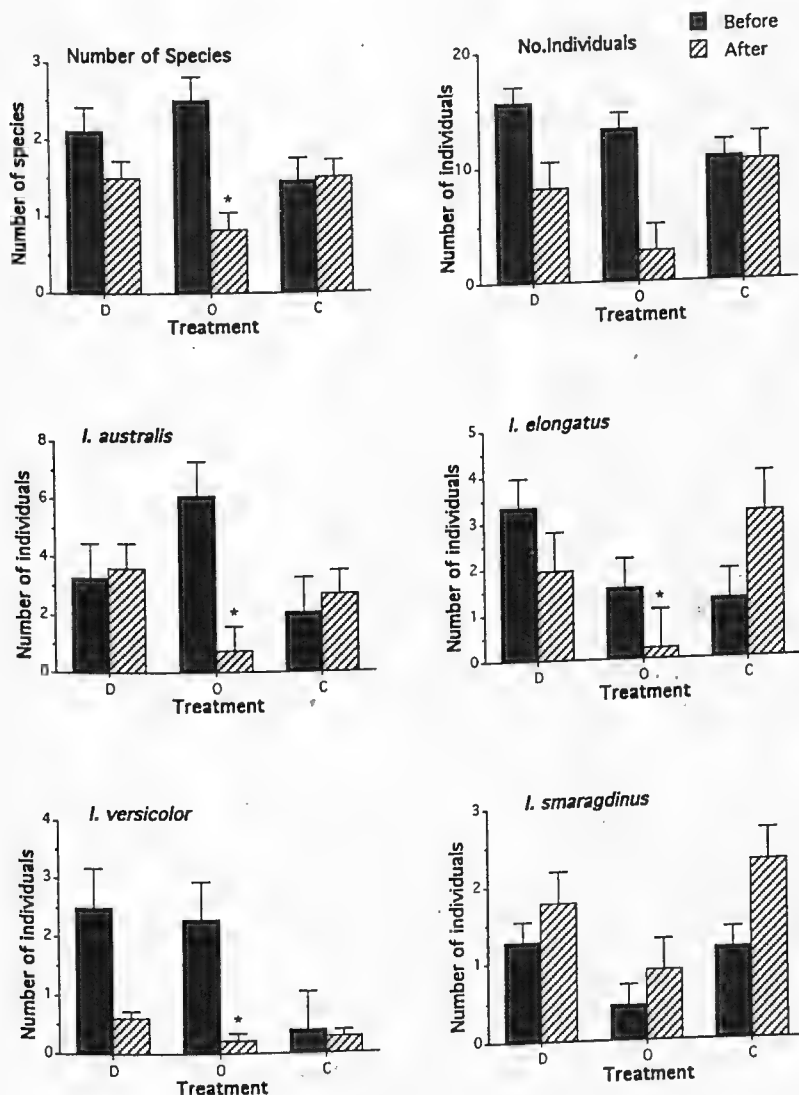Table 4. Analyses of variance of the number of species, total number of individuals, and the numbers *of Ischnochiton australis, Ischnochiton elongatus, Ischnochiton versicolor, and Ischnochiton smaragdinus* found under boulders before and after experimental disturbance. df: degrees of freedom; MS: mean square; *, **: significant at $p<0.05$ and $p<0.01$ respectively; NS: not significant at $p>0.05$; E: term eliminated from model as $p>0.25$.

Source of variation	(df)	Number of chiton species		Number of chiton individuals		I. australis	
		MS	F	MS	F	MS	F
Before/After (B/A)	1	14.52	**	312.96	*	112.67	*
Sites(S)	2	3.19	*	333.72	*	88.22	NS
Treatments(T)	2	1.69	NS	304.39	NS	80.72	NS
B/AxS	2	0.07	NS	7.46	NS	4.67	NS
B/AxT	2	9.02	**	324.24	**	77.06	**
SxT	4	3.24	*	95.53	NS	31.03	NS
B/AxSxT	4	0.24	NS,E	4.16	NS,E	3.97	NS,E
Residual	36	0.93		98.89		28.04	
Total	53						

Source of variation	(df)	I. elongatus		I. versicolor		I. smaragdinus	
		MS	F	MS	F	MS	F
Before/After (B/A)	1	5.35	NS	1.53	*	0.07	NS
Sites(S)	2	11.91	NS	0.97	NS	5.06	NS
Treatments(T)	2	21.63	NS	0.92	NS	35.17	NS
B/AxS	2	1.46	NS	0.06	NS	0.35	NS
B/AxT	2	14.52	**	1.79	**	0.91	NS
SxT	4	5.32	NS	1.39	NS	16.06	NS
B/AxSxT	4	0.38	NS,E	0.09	NS,E	1.19	NS,E
Residual	36	10.02		0.58		11.2	
Total	53						

only differed in the mid-shore with significantly greater densities occurring at Site 3 (Table 2, SNK tests, $p = 0.05$).

The densities of *Cryptoplax mystica* and *Acanthochiton* spp. (Fig. 1) did not vary through time at the Sites in the mid- and low-shore regions and only differed significantly at small spatial scales of Areas nested within Sites (Table 2, analyses of variance, $p > 0.05$ and $p < 0.01$, respectively). *C. mystica* differed between Areas on 6 occasions at the sites in the mid- and low-shore regions (Table 3, SNK tests, $p < 0.05$). The densities of *Acanthochiton* spp. also differed on 3 occasions, but these differences were all confined to Site 4 in the mid-shore (Table 3, SNK tests, $p = 0.05$).

Figure 2.   Mean (± SE) number of species, total number of individuals, and the numbers of *Ischnochiton australis*, *Ischnochiton elongatus*, *Ischnochiton versicolor* and *Ischnochiton smaragdinus* found under boulders disturbed (D), overturned (O) and control (C) boulders at the before and after experimentation. Means of each treatment based on n=18 replicate boulders; * p < 0.05 from SNK tests.

Effects of Disturbance

The Before/After x Sites x Treatments interaction was eliminated from all analyses of variance as the term was not significantly different at $p > 0.25$ (Table 4). This enabled the Before/After x Treatment interaction to be tested over a new Mean Square Residual and resulted in a test with 2 and 40 degrees of freedom giving substantially more power than the original test with 2 and 4 degrees of freedom (Table 4).

The mean numbers of species (Fig. 2) in each treatment were significantly different from Before to After (Table 4, analysis of variance, $p < 0.01$). Treatments were significantly different prior to disturbance, with the least number of species of chitons under control boulders and the largest under overturned boulders (SNK tests, $p < 0.05$). After disturbance, there were significantly fewer numbers of species found under overturned boulders (SNK tests, $p < 0.05$). The Sites x Treatment interaction (Table 7) was due to a significantly greater number of species occurring under the disturbed boulders at Site 3 (SNK tests, $p < 0.05$) prior to disturbance. This result was not unexpected as all boulders were initially chosen at random.

The mean number of individuals (Fig. 2) in each treatment were significantly different prior to disturbance (Table 4, analysis of variance and SNK tests, $p < 0.05$). However, after disturbance there were significantly fewer individuals under the overturned boulders (Fig. 2 and SNK tests, $p < 0.05$). There were also significantly fewer individuals under the disturbed compared to the control boulders, but as this was present prior to disturbance there was no effect of our sampling (SNK tests of pooled means, $p < 0.05$).

The effects of disturbance were also evident with individual species, but was restricted to those species with smaller among boulder variation in their abundances. For example, the mean number of *I. australis* in each treatment (Fig. 2) were significantly different prior to disturbance (Table 4, analysis of variance, $p < 0.05$). After disturbance there were significantly fewer *I. australis* under disturbed and overturned boulders, but only those chitons under the overturned boulders differed from before to after (Fig. 2 and SNK tests, $p = 0.05$). The mean number of *I. elongatus* and *I. versicolor* in each treatment (Fig. 2) were not significantly different prior to disturbance, but after there were significantly fewer individuals of both species under overturned boulders (SNK tests, $p = 0.05$). Treatments were not significantly different prior to disturbance, but after there were significantly fewer individuals of both species under disturbed and overturned boulders (SNK tests, $p = 0.05$). However, the abundances of neither species differed from before to after under the disturbed boulders (SNK tests, $p = 0.05$).

Species such as *I. smaragdinus* (Fig. 2 for example), *C. antiquus* and *C. mystica* exhibited large among boulder variation in their abundances and there were few consistent differences present from before to after and among treatments.

Discussion

Our study has documented the spatial and temporal patterns of abundance of 8 species of chiton occurring under boulders at Long Reef. While most of the early studies (Iredale and Hull 1927, Allan 1950, Dakin 1952, Pope 1943) were primarily concerned with describing the chitons and their associated habitats, they did provide some observations that we were able to test. Early studies suggested that the distribution and abundance of some species were influenced by sediment type. We have shown that the abundance of *I. elongatus* increased with the proportion of fine grained sediment. However, the abundances of other species in this study were not related to sediment type. Relationships between sediment-type and the abundance of chitons have been documented elsewhere. For example, the Californian chiton *Stenoplax heathiana* is only found under boulders that are embedded in sand (Ricketts and Calvin 1968, Andrus and Legard 1975). There are also species such as *Ischnochiton maorianus* that are unaffected by the presence of sediment under the boulder (Mortimer 1985).

Relationships between the size of chitons and the size of the boulder are generally unknown although Andrus and Legard (1975) considered the size of *Stenoplax heathiana* to be unaffected by

boulder-size. The sizes of *Ischnochiton australis* and *Ischnochiton elongatus* were positively correlated with the size of the boulder. It is interesting that this correlation with boulder size should occur with *I. australis* and *I. elongatus* as both species are highly sensitive to boulder disturbance. Overturning a boulder elicited the so-called "escape response" with both species immediately curling up and falling off the boulder. Each chiton is then passively transported by water movement until another boulder reached. Other species, such as *C. antiquus* and *I. smaragdinus* displayed a more sluggish response, showing no immediate reaction but eventually moving slowly to the other side of the overturned boulder. These differences in behaviour have also been noted by other workers (*e.g.* Allan 1950, Ludbrook and Gowlett 1984). It is possible that the correlation between size of the chiton and boulder size is actually determined by the rate of disturbance as McGuinness (1987a) has shown that smaller rocks were overturned more frequently (i.e. ≈ once every 2 months) than were larger rocks (i.e. ≈ once per year). Thus, due to the disturbance-sensitive behaviour of *I. australis* and *I. elongatus*, larger individuals of these species may accumulate under larger boulders, which are less disturbed.

The height on the shore and size of the boulder has also been thought to affect the abundance of particular *Ischnochiton* species (Dakin 1952), but our study did not support this hypothesis and this result was consistent in the mid- and low-shore regions. In contrast, densities of the New Zealand chitons *Ischnochiton maorianus*, *Amaurochiton glaucus*, *Onithochiton neglectus* and *Rhyssoplax* sp. are, on average, greater under large compared to small boulders (Mortimer 1985).

The abundances of under-boulder chitons showed no significant temporal changes over the six months of this study and any temporal variation that was present was far outweighed by the spatial variation. This result was somewhat unexpected as the abundances of many intertidal organisms along the NSW coast exhibit seasonal changes (O'Gower and Meyer 1965, 1971, Underwood 1981b 1984). It is quite conceivable that marked differences in the abundances of under-boulder chitons may only be evident between the cooler and hotter periods of the year. The under-boulder micro-habitat may only be affected by the extremely low Spring tides occurring during daylight hours in Summer and not by those in Winter when very low tides occur at night. Desiccation during low tides coincident with periods of high temperature is thought to cause substantial mortality for chitons (Glynn 1970, Simpson 1976) and its effects are generally more pronounced higher on the shore (Boyle 1970, Horn 1982). Our study was restricted to the cooler, Autumn and Winter months. Sampling over a further two years and at several (at least 2) heights on the shore would be necessary to determine the combined effects of low tides and high temperatures.

The abundances of the platform-dwelling, intertidal organisms on rocky shores of New South Wales can show considerable variation over a horizontal distance of only a few metres (e.g. Underwood 1981a, Underwood and Jernakoff 1981). This is also true for under-boulder communities (McGuinness 1987a, b). The 8 species of under-boulder chiton also exibited similar patterns in that their densities differed at two spatial scales: between areas and sites, 3 m and 60 m apart, respectively. This spatial variation was evident in the mid- and low-shore regions. The tendency towards more fluctuations in the mid-shore may be due to a range of stresses associated with increased emersion and desiccation as well as the greater rate of physical disturbance at sites higher on the shore. A combination of these factors is most likely responsible for the general decrease in abundances and lower diversity of chitons under boulders higher on the shore (McGuinness 1987b).

To our knowledge, our manipulative experiment is the first of its kind to examine the effect of sampling-induced disturbance on populations of under-boulder chitons. Overturning of the boulders resulted in significant declines in species-richness, overall abundances and the densities of *Ischnochiton australis*, *Ischnochiton elongatus* and *Ischnochiton versicolor*. The decline in the abundances of chitons on overturned boulders is consistent with the results for boulder communities in general (McGuinness 1987a, b for Long Reef, and elsewhere Osman 1977, Leiberman *et al.* 1979, Sousa 1979).

There is a number of possible reasons why the overturning of boulders caused a decline in the abundances of chitons. Firstly, overturning may simply result in the active or passive movement of

chitons to undisturbed boulders. For some species, the escape response (see earlier) combined with localised water movement may result in passive movement away from the site of disturbance. Dayton *et al.* (1977) observed a similar escape response when the chitons *Chiton cumingsii, Chiton granosus* and *Acanthopleura echinata* were approached by the predatory starfish *Meyenaster gelatiosus*. When this occurred the chitons were swept away by the surge and re-attached some distance away from the initial disturbance. Mortimer (1985) has argued that the "escape response" may not enhance survival because remaining on a disturbed boulder may not be detrimental. This was definitely not the case for the predatory interactions described by Dayton *et al.* (1977) as failure to escape was detrimental on almost all occasions.

The overturning of boulders could expose the chitons to predation by visual predators such as birds and fish. While several of the local, rocky-reef fish including *Pagrus auratus, Ellerkeldia annulata, Ophthalmolepis lineolatus* and *Cheilodactylus fuscus* are known to consume under-boulder chitons (Russell 1971, Bell 1979, Otway unpubl. data, Smith pers. obs.), we do not know whether their foraging is restricted to the subtidal regions or extends into the intertidal regions during high water.

Secondly, the overtuning of boulders can reduce the area of substratum available for attachment. The upper surfaces of many boulders in the low-shore are covered by foliose macroalgae, reaching 100% cover on occasions (McGuinness 1987a, Smith 1992). On overturning, the algal-covered lower side has a greatly reduced area available for attachment by chitons, particularly for large individuals of *I. australis, I. elongatus* and *I. versicolor* . Small chitons such as *I. smaragdinus*, abundances of which were not affected by overturning, may still find sites for attachment on algal covered boulders.

Finally, the type of micro-habitat found beneath a boulder may also affect distribution and abundance of chitons. For example, rock-type and surface complexity are known to influence the structure of the boulder community at Long Reef (McGuinness 1986). Increased complexity, in the form of pits and grooves, on the under-side of boulders supports more sessile animals, and less complexity resulted in more species of algae. Overturning a boulder can alter the surface complexity by destroying the tubes of polychaetes such as *Diopatra dentata*. Such changes may also affect the chitons as *C. mystica* is frequently found in crevices on boulders, and *Acanthochitona* spp. in small crevices and in between the tubes of polychaetes (Allan 1950, Smith 1992).

Overturning may also alter the micro-habitat in ways that are not readily quantifiable. For example, Pope (1943) noted that *Ischnochiton australis* was frequently found on boulders with a free circulation of water under them. However, the degree of water circulation is difficult to assess quantitatively because sampling may actually impede or alter the water circulation. There are probably many other features of the under-boulder micro-habitat which affect distribution and abundance of chitons. However, to sample the under-boulder community, one must first lift the rock thus altering or destroying the micro-habitat. This is a fundamental problem when working with organisms that occur under boulders.

The manipulative experiment also showed that despite the alterations to the habitat caused by our sampling, the abundances of the under-boulder chitons were not significantly altered indicating that our results were not confounded by sampling-induced disturbance. This result also implies that if sampling is done carefully and boulders are returned as close as possible to their original position and orientation, boulders can be repeatedly sampled with minimal effects on the chiton populations and possibly other organisms. Consequently, we are confident that the abundances documented through time are real and not merely artifacts.

Consideration of sampling-induced disturbance is also relevant to boulder communities in freshwater streams and lakes (*e.g.* Knott *et al.* 1978, Lamberti and Resh 1979, Bunn 1986). It is clear to us that data concerning spatial and temporal patterns of abundance of macro-invertebrates in boulder communities of freshwater streams will be equivocal if the possible confounding effects of sampling-induced disturbance are not addressed. To avoid such problems, it will be necessary to use manipulative experiments, similar to that used here, to identify the effects of sampling-induced disturbance.

Altogether, our study has documented short-term (over 6 months), spatial and temporal patterns in

the abundances of the 6 main species of chiton that occupy the micro-habitats under boulders. The spatial and temporal patterns documented at Long Reef are only indicative of what may be found in other boulder communities along the New South Wales coast. Future research must ensure that other shores are sampled and the results of such studies will indicate whether the patterns observed at Long Reef can be generalised to similar habitats elsewhere. Furthermore, the spatial variation evident in this study demands that future studies will need to incorporate a range of spatial scales in their sampling designs. Failure to do this will, most likely, disguise patterns associated with different levels of patchiness within these communities. Finally, a greater understanding of the ecology of under-boulder chitons will require demographic studies and the use of manipulative field experiments to identify the proximal causes of patterns in space and time.

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Growth of the hairy mussel, *Trichomya hirsuta* (Lamarck 1819), from eastern Australia

C. L. Goggin

Dept Parasitology, The University of Queensland, Brisbane 4072 Qld Australia

Abstract

Hairy mussels, *Trichomya hirsuta*, were held in cages on the east coast of Australia at Townsville, Brisbane, Port Stephens, Lake Macquarie and Eden. Growth rates of the mussels were estimated using the von Bertalanffy equation using length measurements alone and an index of height, length and breadth. The growth rate estimates (K) varied with season and were highest in summer at all sites. Highest growth rates for *T. hirsuta* over a 52 week period were recorded at Lake Macquarie from both length measurements and the index of height, length and breadth. Highest growth rates for the total sampling period were recorded from Brisbane. *Trichomya hirsuta* reached its asymptotic length at Lake Macquarie in 10 to 25 years with growth rates of 2.7–9.0mm/year.

Introduction

The hairy mussel, *Trichomya hirsuta* (Lamarck 1819), is found from Townsville to Tuross on the east coast of Australia, and from South Australia and the Great Australian Bight (Iredale, 1939; Cotton, 1961). The mussel forms thick masses or clumps (Laseron, 1956) which occur on muddy bottoms, sea grass beds and attached to artificial structures (Robinson and Gibbs, 1982). *Trichomya hirsuta* prefers a truly marine environment, but can penetrate into regions of low salinity (Jenkins, 1976). Despite the wide distribution and massive stable populations of *T. hirsuta* which occur in Australian waters, little is known of the biology of this species.

Trichomya hirsuta is reported to have slow growth with pronounced seasonality in Lake Macquarie (Hum, 1971). My study extended these observations and investigated latitudinal and seasonal variation in growth rates of hairy mussels along the east coast of Australia.

Materials and Methods

Mussels were collected 100m offshore at Vales Point, Lake Macquarie, NSW (Fig.1), in approximately 3.5m of water. At this site, mussels form clumps of several hundred individuals on the muddy bottom and were considered to belong to a single population. Mussels between 8 and 80mm shell length were selected from different clumps and tagged using plastic, numbered tags, 5mmx3mm, attached with a cyanoacrylate adhesive ("Loctite" Superfast IS495 Cat. No. 49580) on the posterior of the left valve.

Cages (0.3x0.3x0.75m) were made of galvanised weldmesh (1.6mm wire diameter, 10mm square aperture) with five fibro-cement shelves. The mesh was removed from two shelves to assess the effect of the mesh on growth of the mussels. The mussels on shelves without mesh are hereafter referred to as "uncaged". Sixty tagged mussels were placed on each of the upper four shelves and covered with commercial mussel socking until they attached to the asbestos-cement plates with byssal threads. The bottom shelf was left empty in all cages.
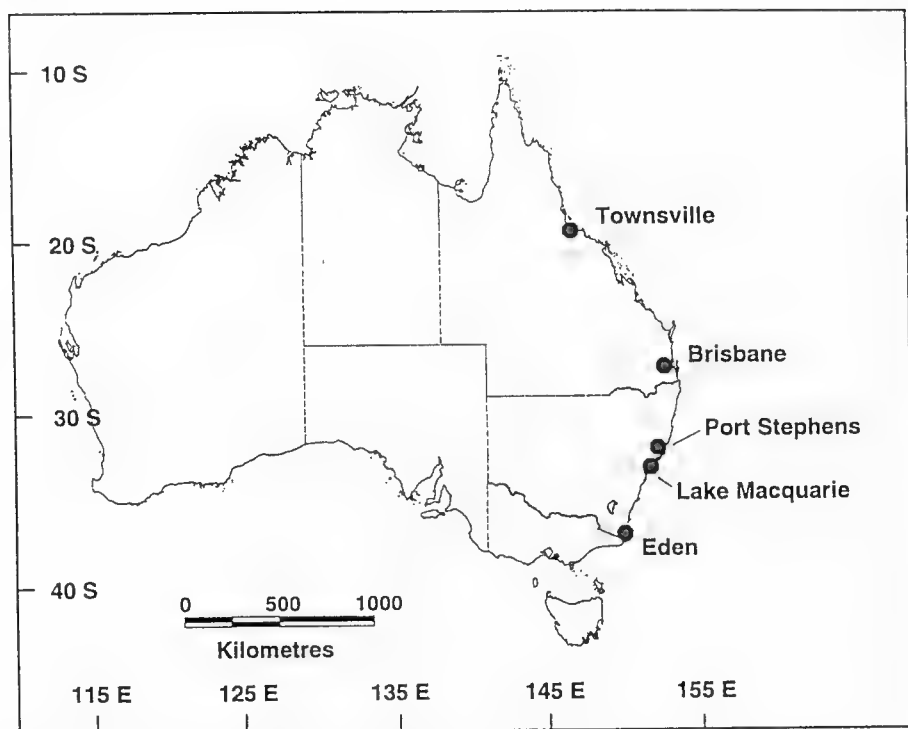
Figure 1.   Location of cages with tagged hairy mussels, *Trichomya hirsuta*, along the east coast of Australia

Cages were located at five sites on the east coast of Australia: Townsville, Brisbane, Port Stephens, Lake Macquarie and Eden (Fig. 1). They were permanently submerged at approximately 3m depth and located close to populations of wild, hairy mussels. The cage at Townsville was hung under a commercial tanker wharf; at Brisbane, the cage was attached to a disused oyster lease in a swift flowing channel; at Port Stephens and at Eden, the cages were suspended from an anchored raft; and at Lake Macquarie, it was placed in the inlet canal of a power station. Height, length and breadth of each tagged mussel was measured every 12 weeks, except in Brisbane and Townsville (Table 1) with Vernier calipers to the nearest 0.1mm.

Growth was estimated using von Bertalanffy regression plots of initial length versus length increment. The slope of the regression plot is $-(1-e^{-K})$ where K= Brody growth coefficient (Ricker, 1975) and is a measure of the rate of decrease of growth. The asymptotic length (L_∞) is estimated from the intercept of the regression line with the x-axis.

For all sites, the growth coefficient (K) and asymptotic length (L_∞) were calculated from length data of: caged; and uncaged mussels, and for: each sampling interval; 4 weeks (results not shown) and 52 weeks. The K and L_∞ of caged and of uncaged mussels were compared by t-test when K was at a maximum. The slopes of the regression lines did not differ significantly (p>0.05 at all sites), so the results for caged and uncaged mussels from one site were combined in further analyses. K and L_∞ values were re-estimated for periods of 4 weeks and 52 weeks using length data from each sampling interval and the total sampling period. The K and L_∞ values estimated for the total sampling period were calculated using all length measurements which were taken two sampling periods apart. This method estimated growth of mussels more accurately than averaging seasonal growth rates because, in some cases, growth was not detectable over a single sampling period. Growth in mm/year was

Table 1. Asymptotic lengths (L_∞) of hairy mussels, *Trichomya hirsuta*, held in cages at five sites estimated from plot of length increment versus initial length at various sampling dates. TOTAL estimated from all length measurements taken two sampling periods apart.

CAGE SITE	SAMPLING DATES	SAMPLING INTERVAL (weeks)	L_∞ (mm)
TOWNSVILLE	25/5/82–19/8/82	12.3	65.0
	19/8/82–10/11/82	11.9	65.9
	10/11/82–10/2/83	13.1	70.8
	10/2/83–27/4/83	18.9	100.7
	TOTAL	56.2	67.7
BRISBANE	19/5/82–29/9/82	20	72.4
	29/9/82–29/7/83	43	74.1
	TOTAL	63	70.7
PORT STEPHENS	6/6/82–29/8/82	12	75.1
	29/8/82–29/11/82	12	65.4
	29/11/82–13/2/83	12	74.1
	13/2/83–8/5/83	12	82.0
	TOTAL	48	75.6
LAKE MACQUARIE	19/4/82–12/7/82	12	73.9
	12/7/82–4/10/82	12	77.7
	4/10/82–27/12/82	12	63.1
	27/12/82–17/3/83	12	70.8
	TOTAL	48	67.2
EDEN	15/4/82–8/7/82	12	746.5
	8/7/82–30/9/82	12	51.7
	30/9/82–23/12/82	12	57.0
	23/12/82–14/3/83	12	76.6
	TOTAL	48	60.7

calculated from the K and L_∞ values estimated from these data using $dL/dT = K(L_\infty - L_t)$ mm/month.

Height (H), length (L) and breadth (B) were summed for individual mussels to give an index (HLB) which was used to determine K and L_∞ values by plotting change in HLB against initial HLB. These indices were compared to values estimated from length alone.

Growth of the mussels was tested for an exponential phase using a plot of initial length versus length increment. Mussels in an exponential growth phase i.e.below the inflection point of the sigmoid growth curve, generate a positive slope, while at the inflection point there is no correlation, and above this the normal negative slope is generated.

Length versus time of the Lake Macquarie caged population was plotted. This von Bertalanffy plot was generated from

$$L_t = L_\infty (1 - e^{-K(t_1 - t_0)}) \qquad \text{(Yamaguchi, 1975)}$$

where L_∞ = ultimate length, K= growth coefficient, t_0= theoretical age at which length is 0 (t_0 was assumed to be 0).

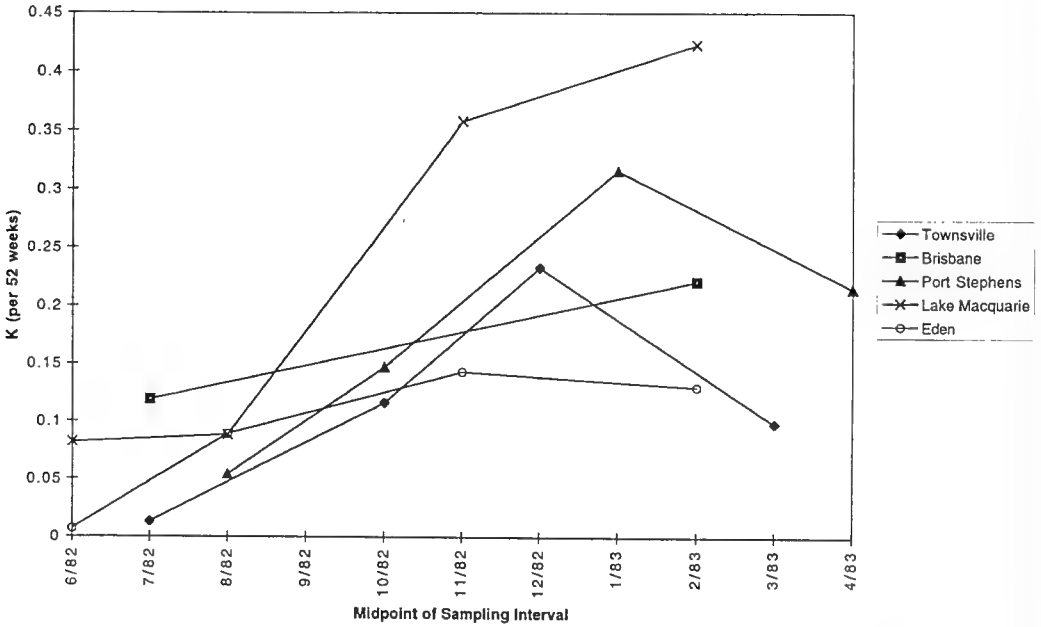Results were analysed using the Statistical Package for the Social Sciences (SPSS 80).

Figure 2.   Growth rate (K) estimates for 52 weeks calculated from the von Bertalanffy equation using length (mm) measurements of hairy mussels, *Trichomya hirsuta*, held in cages along the east coast of Australia versus time.
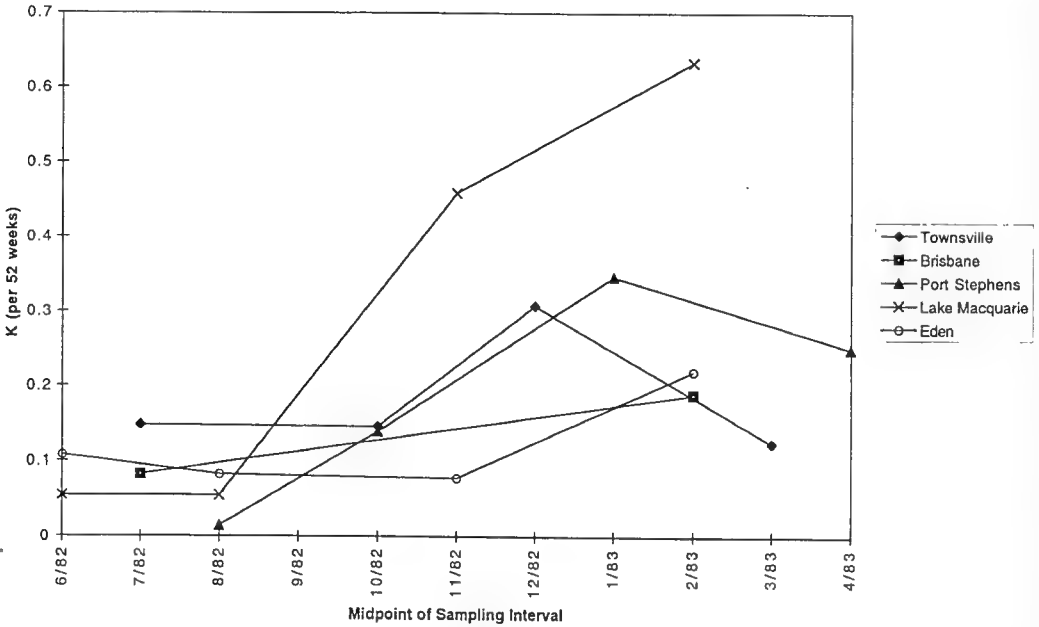

Figure 3.   Growth rate (K) estimates for 52 weeks calculated from the von Bertalanffy equation using an index of height, length and breadth (HLB) measurements of hairy mussels, *Trichomya hirsuta*, held in cages along the east coast of Australia versus time.

Results

The von Bertalanffy equation overestimates growth in sedentary marine invertebrates in the early, exponential phase of growth (Yamaguchi, 1975) and therefore is valid only for growth beyond one third of the asymptotic length (Theisen, 1975). There were no mussels from Lake Macquarie found in an exponential growth phase. Mussels at the inflection point were considered to produce a valid point on the curve and were included in further analyses. Thus, the von Bertalanffy equation estimated growth accurately in this population.

Growth rates (K) were highest during the summer at all sites with the highest values recorded at Lake Macquarie (K=0.423 from length measurements; Fig. 2) (K=0.634 from HLB; Fig. 3). The slowest growth in length was recorded in winter at the extremes of *T. hirsuta* distribution at Townsville (K=0.013) and Eden (K=0.007) (Fig. 2) and in an index of height, length and breadth (HLB) in winter at Port Stephens (K=0.014, Fig. 3). Slow growth rates resulted in an overestimation of L_∞ (e.g. Eden for 15/4/82–8/7/82, Table 1).

The highest K values for the total sampling period were estimated from HLB at Lake Macquarie (K=0.634) and from length measurements alone at Brisbane (K=0.205) (Fig. 4).

No significant differences (p> 0.05) were found between predictions of K calculated from HLB (Fig. 3) and those calculated from length alone (Fig. 2), except at Lake Macquarie. There were significant differences (p> 0.05) in growth of breadth of hairy mussels from Lake Macquarie compared with length and height. Length, breadth and height of mussels were changing at the same rate at all other sites.

Smaller mussels grew faster than larger mussels as determined from the plot of initial length versus length increment. A plot of residuals of the regression of initial length versus length increment revealed no trends. The growth of hairy mussels from Lake Macquarie varied with initial length of mussels. Mussels of initial length 10mm grew 8.98mm/year; those at 20mm grew 7.41 mm/year; those at 30mm grew 5.84mm/year; those at 40mm grew 4.27mm/year and those at 50mm grew 2.70mm/year.
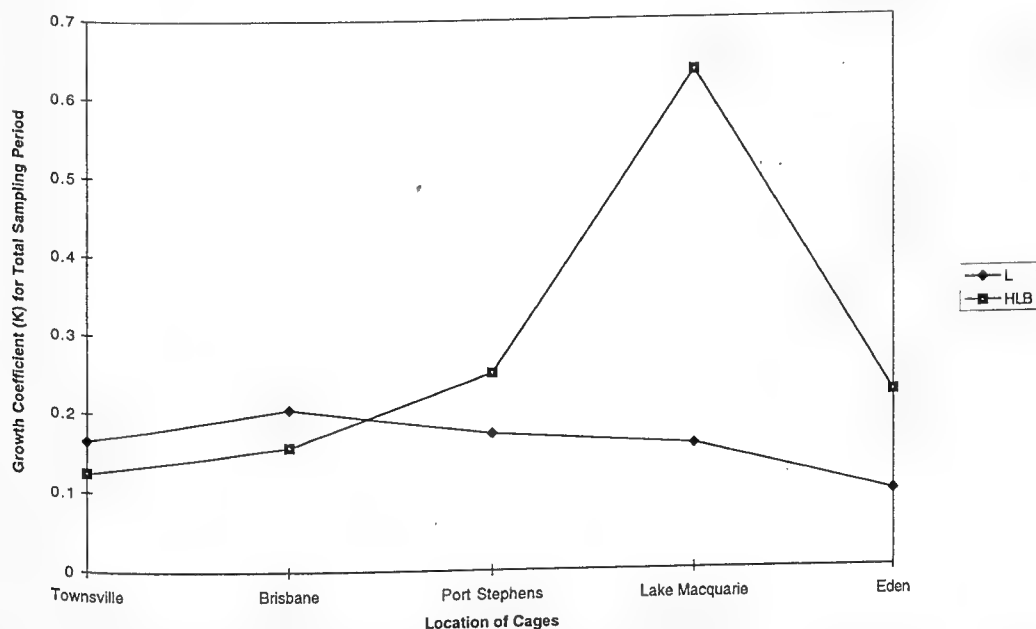

Figure 4.   Growth rate (K) estimates for total sampling period of hairy mussels, *Trichomya hirsuta*, held in cages at five locations on the east coast of Australia.
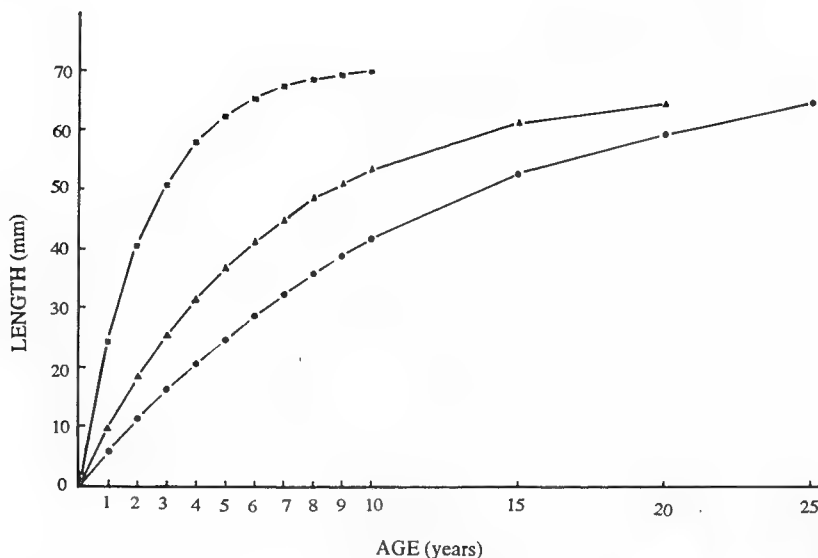
Figure 5.   Age estimates from caged, tagged hairy mussels, *Trichomya hirsuta*, from Lake Macquarie. ■ K=0.423, L_∞ =70.8 (27/12/82–17/3/83); ▲ K=0.095, L_∞ =67.2 (total sampling period); ● K=0.082, L_∞ =73.9 (19/4/82–12/7/82).

There were significant initial mortalities at Brisbane and Townsville which decreased over the sampling period (Fig. 5). Mortalities decreased with time at Townsville, Brisbane and Port Stephens and were low at Port Stephens and Eden throughout the experiment. High initial mortality recorded from Brisbane and Townsville cages may result from loss of mussels from uncaged shelves before they were attached and is not considered to reflect mortalities in wild populations. Mortalities were high at Lake Macquarie on the 36 week measurement when the cage was heavily fouled and mussels starved or suffocated under the sediment.

Discussion

Hairy mussels, *Trichomya hirsuta*, grew slowly on the east coast of Australia, with rates increasing in summer. Mussels grew best at Lake Macquarie and Brisbane. Estimates of growth of mussels in Lake Macquarie were similar to estimates made for *T. hirsuta* by Hum (1971) (K=0.26) who also recorded seasonal variation in growth rates for the hairy mussel in Lake Macquarie.

The growth of mussels at Townsville and Eden may have been affected adversely by local environmental conditions: Eden is at the southern, and Townsville at the northern, limit of wild hairy mussel populations on the east coast of Australia. Furthermore, in Townsville, the cage was located under an oil tanker wharf and may have been affected by pollution. In Townsville, low salinities occur during the summer wet season and water temperatures may reach above 28°C (Kenny, 1974) which is the upper lethal temperature for *T. hirsuta* (Wallis, 1976). These conditions are likely to retard the growth of mussels in Townsville and account for low K values during summer.

Trichomya hirsuta grows much slower than the blue mussel, *Mytilus edulis* in Australia and overseas. In Australia, *Trichomya hirsuta* grew slower than *M. edulis* held in cages at the same sites. Body (1983) calculated K values for a 12 week period for *M. edulis* from Eden of 0.08 to 0.58 (c.f. K=0.002 – 0.033 for *T. hirsuta*) and from Port Stephens of 0.07 to 0.26 (K=0.012 – 0.073 for *T. hirsuta*). The highest K values at Port Stephens for *T. hirsuta* were similar to the lowest K values for *M. edulis*. *Trichomya hirsuta* grows at a similar rate in Brisbane (K=0.12 – 0.2) to *M. edulis* in
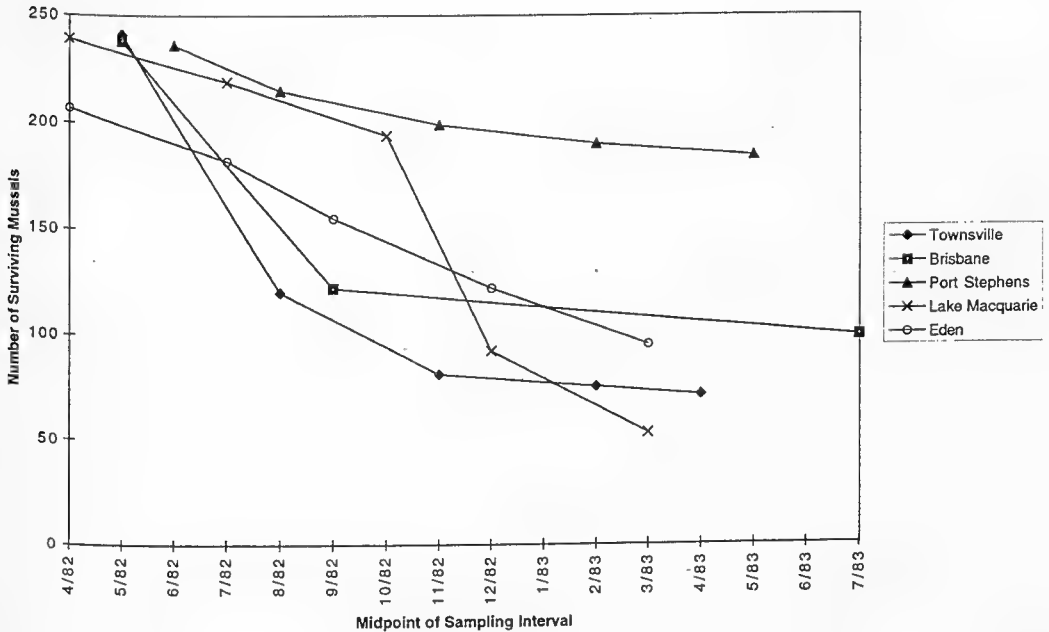
Figure 6.   Number of hairy mussels, *Trichomya hirsuta*, which survived in cages along the east coast of Australia with time.

Danish fjords (K=0.14 and 0.97) (Theisen, 1975) and in Townsville it grows at a similar rate (K=0.01 – 0.23) to *M. edulis* in Greenland (K=0.02 – 0.16) (Theisen, 1973).

Growth estimates (K) from HLB did not differ significantly from those calculated from length alone, except at Lake Macquarie, where breadth was growing differently to the other two measures. High water movement at Lake Macquarie and Brisbane did not cause an increase in the growth of breadth of the mussels in the latter site. The cause of the difference in growth of breadth of mussels at Lake Macquarie is unclear. Seed (1973) found breadth often exceeds height in older *M. edulis*. The size of mussels at Lake Macquarie was not different to mussels at other sites.

Caging did not affect growth of *T. hirsuta*. Kautsky (1982) found growth increased from 2.2– 3.1mm/year in natural populations of mussels to 15mm/year in his cages. It is possible that *T. hirsuta* in cages in this study grew more rapidly than natural populations because there were lower densities of mussels and they were higher in the water column, than wild populations. Any increase in growth of hairy mussels, however, may be offset by a decrease in growth due to handling (Stromgren,1976).

The von Bertalanffy plot estimated a range of ages for *T. hirsuta* in Lake Macquarie because the growth rate varied with season. *Trichomya hirsuta* reach 50mm long between 4 and 14 years and reach 95% of their asymptotic length between 10 and 25 years. MacIntyre (1959) estimated growth rates of 10–40mm/year for *T. hirsuta* from Lake Macquarie which are higher than estimated in this study. It is possible that MacIntyre (1959) selected small mussels which grow faster than larger individuals and would account for the discrepancy in estimated growth rates. Growth of *T. hirsuta* in this study was similar to mussels in Hudson Bay and Greenland which reached 50mm in 7–11 years (Theisen, 1973). The highest growth rates of *T. hirsuta* were similar to those of *M. edulis* on exploited mussel beds in Europe which reach 50mm in 2–4 years (Theisen, 1973).

Trichomya hirsuta grows slowly with pronounced seasonality on the east coast of Australia. The highest growth rates of the hairy mussel occur in the middle of its range with rates decreasing toward the limits of its distribution.

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Nomenclatural Rectifications in Australian Hydrobiidae

W. F. Ponder

Australian Museum, 6 College Street,
Sydney, NSW 2000, Australia

The purpose of this note is to rectify the nomenclature of a genus and a species of Australian Hydrobiidae. The name *Dalhousia* Ponder *et al.* 1996, erected in the last issue of this journal, is preoccupied and requires a replacement name which is given below. The opportunity is also taken to point out an earlier name for a common estuarine hydrobiid revised by Ponder and Clark (1988).

Caldicochlea new name

Dalhousia Ponder et al., 1996 not *Dalhousia* McIntosh, 1885:186 (Annelida).

Derivation: *Caldus* – Latin, warm, hot. *Cochlea* – Latin, snail. Refers to the hot spring habitat of many of the populations of these snails.

Caldicochlea is restricted to Dalhousie Springs, northern South Australia.

Ascorhis tasmanica (Martens 1858). Fig. 1.

Hydrobia tasmanica Martens 1858: 185, pl. 5, fig. 12.

Bythinia victoriae Tenison-Woods 1878: 65.

Ascorhis victoriae.– Ponder & Clark, 1988:664–666 (see for remainder of synonymy).

In the process of examining type material of Australian freshwater hydrobiids, the types of *Hydrobia tasmanica* were examined and found to be identical to the common estuarine *A. victoriae.* The recognition of the status of this species has had a chequered history. *H. tasmanica* has been previously wrongly regarded (eg. May, 1921 Iredale, 1943) as a freshwater species and was included
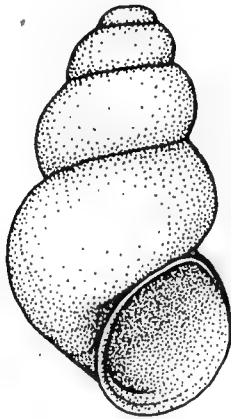

Figure 1. *Ascorhis tasmanica*.Syntype of *Hydrobia tasmanica*. Scale 1mm.

in *Fluvidona* by Smith (1992). May (1921) wrongly included several freshwater species in the synonymy of *H. tasmanica* (as *Potamopyrgus*), as well as correctly including *P. victoriae*. Gabriel (1939) included *H. tasmanica,* along with *P. victoriae* and several freshwater taxa, in the synonymy of *Bithinella buccinoides* (Quoy & Gaimard 1835), a species now known to be an *Assiminea* (see Ponder & Clark, 1988). Iredale (1943) incorrectly included three names based on freshwater taxa in the synonymy of *H. tasmanica* which he included in *Rivisessor.*

Dimensions	Length (mm)	Width (mm)	Aperture length (mm)	Number of teleoconch whorls
Figured syntype	2.22	1.26	0.86	3.25
Syntypes	1.83	1.18	0.79	2.70
	2.35	1.47	1.04	3.10

Syntypes (3) in Naturhistorisches Museum, Wien (Vienna), no. 31729.

Ascorhis tasmanica is an abundant species in estuarine conditions in south eastern Australia, its range extending from western South Australia to southern Queensland. Ponder & Clark (1988) note an inland record from a brackish pool in South Australia (near Lake Eyre South, in a pool of The Margaret, near Old Billa Kalina Homestead ruins). Recently a second population has been located by D. Niejalke in the same area, in Francis Swamp.

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A luminescent eulimid (Mollusca: Gastropoda) from New Zealand

Bruce A. Marshall

Museum of New Zealand Te Papa Tongarewa
P.O. Box 467, Wellington, New Zealand

A new species of *Melanella* is described from New Zealand. The last turn of the body emits a lime yellow glow, the first record of luminescence in Eulimidae and the first record of yellow luminescence in a gastropod (otherwise blue). It is parasitic on the holothurian *Ocnus brevidentis* (Hutton, 1872). *Melanella archeyi* (Finlay, 1928) and *M. aucklandica* (Suter, 1909) are recognised as distinct species, and outer lip profiles of the holotypes are illustrated.

Introduction

During a recent visit to Preservation Inlet, Fiordland, New Zealand, C.D. Paulin (Museum of New Zealand, Wellington) collected specimens of a eulimid that had been previously seen there parasitising an abundant, small, red holothurian (Fig. 1). The living eulimids proved easy to see because the last turn of the soft parts glowed luminescent lime yellow through the translucent shell (C.D. Paulin, pers. comm.). The luminescence (apparently intracellular) was continuous and restricted to the last (white in alcohol) turn of the body, where no specific site was apparent. This is the first record of luminescence in a eulimid, and the first record of lime yellow luminescence in a gastropod (otherwise blue – Nicol, 1964). The holothurian was identified (by D.L. Pawson) as the red (*carnleyensis* Dendy, 1909) form of *Ocnus brevidentis* (Hutton, 1872), which is widely distributed off New Zealand (Pawson, 1970), and abundant in Preservation Inlet, Fiordland, the type locality of the new eulimid.

Systematics

### Family Eulimidae H. and A. Adams, 1853

Genus *Melanella* Bowdich, 1822

*Melanella* Bowdich, 1822: 27. Type species (monotypy): *Melanella dufresnii* Bowdich, 1822.

Melanella luminosa n. sp.

(Figs 1–5)

Description. Shell up to 5.75 mm high, tall, slender, narrowly and evenly conical, straight, height/diameter ratio 0.36–0.41 (mean 0.38), stout, perfectly smooth, translucent, colourless. Protoconch of about 1.5 convex whorls, 530 μm wide, exposed part 630 μm high, contour perfectly continuous with teleoconch, demarcated from teleoconch by growth scar. Teleoconch of up to 8.8 weakly convex whorls, 4 or 5 incremental scars at varying positions. Aperture small, ovate. Outer lip profile markedly prosocyrt-opisthocline. Columella almost straight. Last whorl of soft parts (white in ethanol) of living animal glowing luminescent lime yellow through translucent shell.
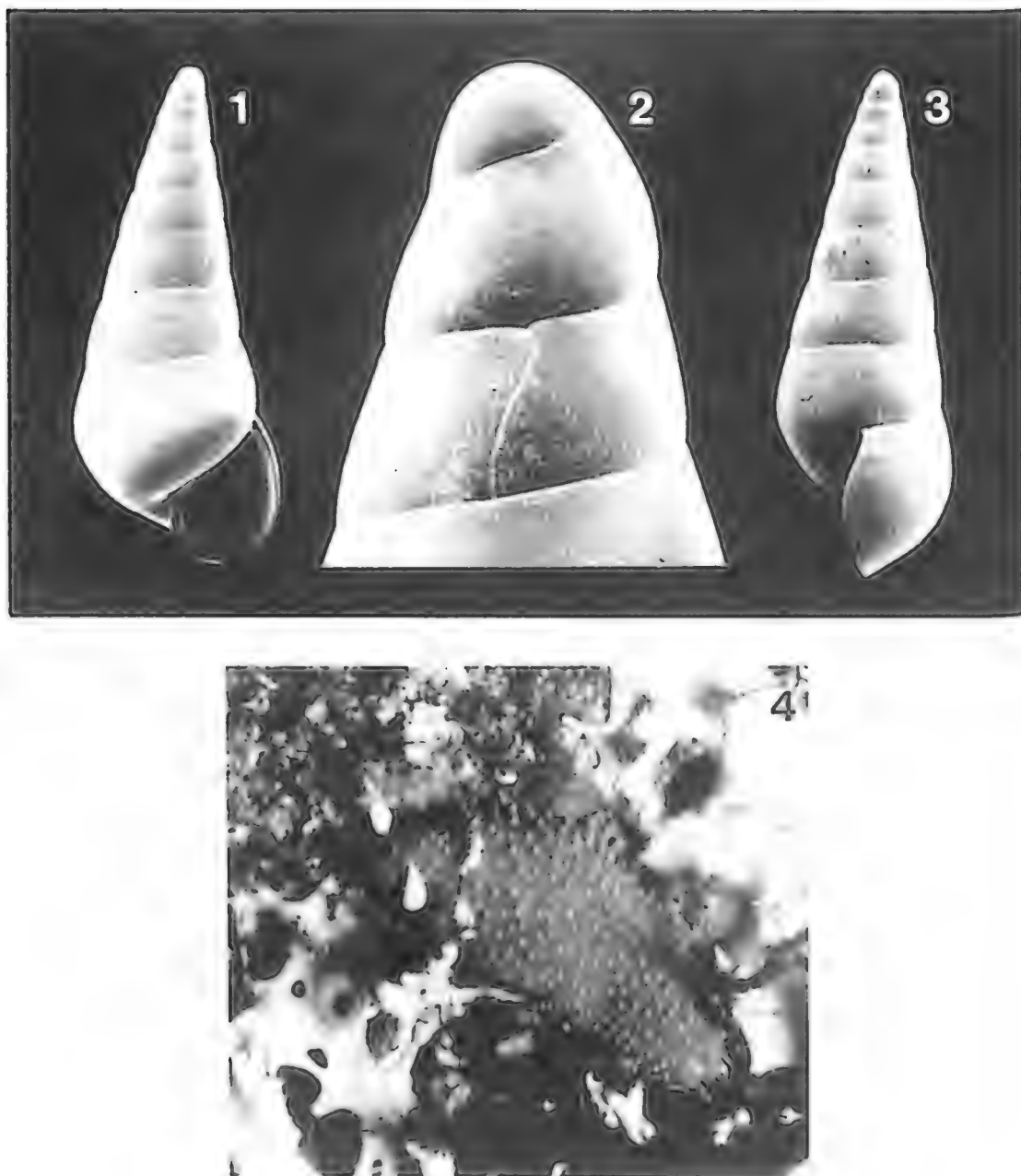
Figures 1–4.   *Melanella luminosa*. 1. Holotype, apertural view, 5.75 x 2.25 mm. 2. Protoconch (height 630 μm) of paratype, NMNZ M.131687. 3. Holotype, lateral view showing outer lip profile. 4. Two adults parasitising *Ocnus brevidentis* (Hutton, 1872) at type locality (from colour slide courtesy P. Ryan).
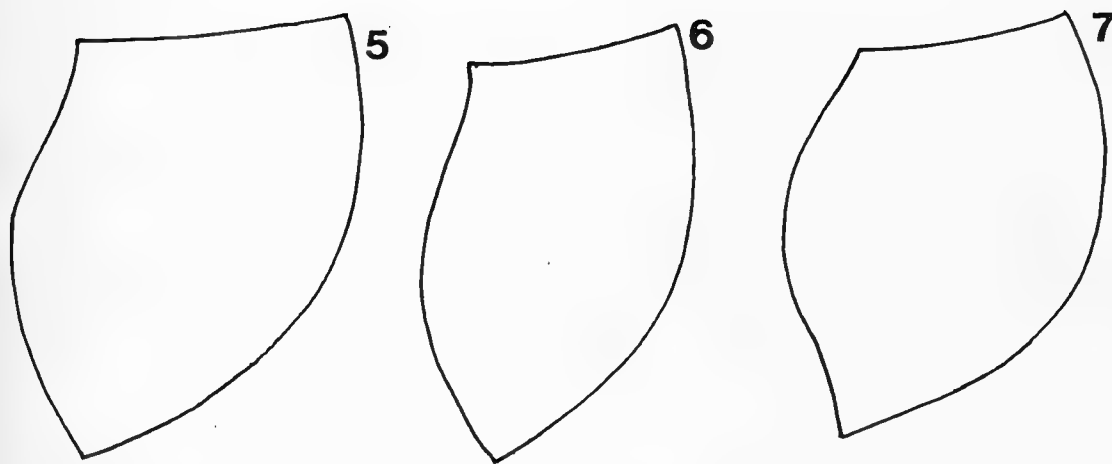
Figures 5–7.   Camera lucida outlines of outer lip profiles of *Melanella* species. 5. *Melanella luminosa*, holotype, lip height 1.80 mm. 6. *Melanella aucklandica* (Suter, 1909), holotype, Auckland Islands, lip height 1.85 mm. 7. *Melanella archeyi* (Finlay, 1928), holotype, Chatham Islands, lip height 1.15 mm.

Type data. Holotype Museum of New Zealand, Wellington (NMNZ M.131738) and 15 paratypes – NMNZ (12, M.131687), Australian Museum, Sydney (1), Swedish Museum of Natural History, Stockholm (2): 46°03.2'E, 166°44.1'E, "Strawberry Fields", opposite Adam Head, Narrow Bend, Long Sound, Preservation Inlet, Southland, New Zealand, alive, parasitising the red (*carnleyensis* Dendy, 1909) form of the holothurian *Ocnus brevidentis* (Hutton, 1872), 15–18 m, 18 August 1996, C.D. Paulin.

Other material examined (25 specimens NMNZ): 44°04'S, 175°23.5'W, E of Forty Fours, Chatham Islands, dead, 238 m, 1 February 1954, m.v. *Alert* (1, M.10567); "The Gut", Bauza Island, Doubtful Sound, Fiordland, dead, 53 m, 16 February 1987, scuba, G.S.Hardy (12, M.131740); off Passage Point, Dusky Sound, Fiordland, dead, 22–27 m, 8 January 1952, m.v. *Alert* (3, M.14693); between Unnamed Island and Breaksea, Dusky Sound, dead, 37 m, 7/5/1950, m.v. *Alert* (4, M.13855); off Chalky Island, Chalky Inlet, Fiordland, dead, 37 m, 6/5/1950, m.v. *Alert* (1, M.13978); 46°02.95'S, 166°43.80'E, "38 fathom bay", Isthmus Sound, Preservation Inlet, Fiordland, dead, 10–18 m, 25 March 1993, scuba, A.L. Stewart, C.D. Paulin & C.D. Roberts (4, M.131737).

Distribution. Southern fiords of Southland and Chatham Islands, New Zealand, 10–238 m, taken alive at 15–18 m; external parasite of the holothurian *Ocnus brevidentis* (Hutton, 1872).

Remarks. *Melanella luminosa* closely resembles both *M. aucklandica* (Suter, 1909) and *M. archeyi* (Finlay, 1928). It resembles *M. aucklandica* (holotype Canterbury Museum, Christchurch M5489 – Fig. 6) in size relative to the number of whorls, and differs mainly in that the outer lip is more strongly prosocyrt in profile, but also in attaining slightly smaller size (height 5.75, cf. 6.15 mm), and in being slightly more broadly conical (height/width ratio 0.36–0.41, mean 0.38; cf. 0.34–0.37, mean 0.35). It resembles *M. archeyi* (holotype Auckland Institute and Museum AK70288 – Fig. 7) in having a rather strongly opisthocline outer lip, but differs in attaining larger size (*M. archeyi* up to 4.20 mm high), and in being larger relative to the number of whorls (height 4.30 mm and 7 whorls for paratype of *M. luminosa*, cf. 4.20 mm and 8 whorls for holotype of *M. archeyi*). Most specimens of *M. archeyi* differ further in having slightly but distinctly more strongly convex teleoconch whorls. *M. archeyi* was treated as a synonym of *M. aucklandica* by Powell (1979), though it now seems clear that they are distinct species. All three *Melanella* species are widely distributed in southern New Zealand (NMNZ): *M. aucklandica* from Foveaux Strait, Pukaki Rise, and Stewart,

Auckland, Antipodes and Chatham islands, 0–140 m; *M. archeyi* from Stewart Island, outer coast of southern Fiordland, and the Chatham Islands, 0–15 m; *M. luminosa* from southern Fiordland and the Chatham Islands, 10–238 m. The host of *M. aucklandica* and *M. archeyi* is unknown, but as with other *Melanella* species it is sure to be holothurian (Warén, 1984), perhaps *Ocnus brevidentis*, which has a similar distribution in southern New Zealand (Pawson, 1970).

M. luminosa, M. aucklandica and *M. archeyi* are similar to the type species of *Melanella* (Heppell, 1995) and to other species referred there by Warén (1984).

Bioluminescence is rare in marine gastropods, and has been recorded only from some species of Planaxidae (Haneda, 1958; Houbrick, 1987; Ponder, 1988), a *Tonna* species (Tonnidae) (Haneda, 1958), and a few nudibranchs (Harvey, 1952; Nicol, 1964). Precisely which part of the anterior anatomy luminesces, the mode of light generation, the reason for luminescence, and the significance of lime yellow over blue light emission in *Melanella luminosa*, remains to be determined.

Etymology. Full of light (Latin).

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Pectinoidea (Mollusca: Bivalvia: Propeamussiidae: Pectinidae) of Lord Howe Island, Norfolk Island and the Kermadec Islands

Henk H. Dijkstra

Zoological Museum Amsterdam
P O Box 94766, 1090 GT Amsterdam
The Netherlands

and

Bruce A. Marshall

Museum of New Zealand Te Papa Tongarewa
P O Box 467, Wellington
New Zealand

Abstract

Twenty-four pectinoidean species are recorded from Lord Howe Island (7 species), Norfolk Island (13 species) and the Kermadec Islands (14 species). Eighteen species are new records, and these are compared with similar species from the Australasian region. The following taxa are newly synonymised: *Annachlamys leopardus rena* Iredale, 1939 (= *A. kuhnholtzi* (Bernardi, 1860)), *Chlamys cellularis* Oliver, 1915 (= *C. c. coruscans* (Hinds, 1845)), *Chlamys (Mimachlamys) asperrimoides* Powell, 1958 (= *M. senatoria* (Gmelin, 1791)). *Chlamydella favus lemchei* Powell, 1958 is considered to be specifically distinct from *Cyclopecten favus* Hedley, 1902, and is referred to *Cyclochlamys* Finlay, 1926. Lectotypes are for the following species designated: *Hemipecten forbesianus* A. Adams & Reeve, 1849, *Ostrea senatoria* Gmelin, 1791, and *Ostrea porphyrea* Gmelin, 1791.

Introduction

In his monograph on the molluscan fauna of the Kermadec Islands Oliver (1915) recorded three Pectinoidea, of which one was new for science (*Chlamys cellularis*). Subsequently, Powell (1958) introduced four additional species obtained by the "Galathea" Expedition (1952) from off the Kermadec Islands and Norfolk Island.

Twenty-four pectinoideans are here recorded from the study region: Lord Howe Island (7 pectinids), Norfolk Island (5 propeamussiids and 8 pectinids), Kermadec Islands (9 propeamussiids and 5 pectinids). Of these, 5 are new records for Lord Howe Island, 9 for Norfolk Island, and 8 for the Kermadec Islands.

The following abbreviations are used: AIM, Auckland Institute and Museum; AMS, The Australian Museum, Sydney; BMNH, The Natural History Museum, London; CM, Canterbury Museum, Christchurch; IOAS, Institute of Oceanology, Academia Sinica, Qingdao; MNHB, Museum für Naturkunde der Humboldt-Universität, Berlin; MNHN, Muséum National d'Histoire Naturelle, Paris; NMNZ, Museum of New Zealand, Wellington; NZOI, National Institute of Water and Atmospheric Research, Wellington; OUZM, Oxford University Zoology Museum, Oxford; QVM, Queen Victoria

Museum and Art Gallery, Launceston; SAM, South Australian Museum, Adelaide; SMNH, Swedish Museum of Natural History, Stockholm; USNM, National Museum of Natural History, Washington D.C.; WAM, Western Australian Museum, Perth; ZMA, Zoölogisch Museum, Amsterdam; ZMUC, Zoologisk Museum, Copenhagen; ZSI, Zoological Survey of India, Calcutta; lv, left valve(s); rv, right valve(s); v, valve(s); pr, conjoining valves.

Systematics

Superfamily Pectinoidea Wilkes, 1810

Family Propeamussiidae Abbott, 1954

Genus *Propeamussium* de Gregorio, 1884

Propeamussium de Gregorio, 1884: 119. Type species (by original designation): *Pecten (Propeamussium) ceciliae* de Gregorio, 1884; Miocene, Sicily, Italy.

Paramusium Verrill, 1897: 72. Type species (by original designation): *Amussium dalli* E. A. Smith, 1885; Recent, W Atlantic.

Occultamussium Korobkov, 1937: 56. Type species (by original designation): *Pecten semiradiatus* Mayer, 1861; Upper Eocene, Tirol, Austria.

Pseudopalliorum Oyama, 1944: 244. Type species (by original designation): *Pecten interradiatus* Gabb, 1869; Eocene, California, U.S.A.

Bathymussium Oyama, 1951: 79. Type species (by original designation): *Amussium jeffreysii* E. A. Smith, 1885; Recent, N Sulu Sea, Philippines.

Micramussium Oyama, 1951: 50. Type species (by original designation): *Ctenamusium (Micramussium) siratama* Oyama, 1951; Recent, Sagami Sea, Japan.

Flavamussium Oyama, 1951: 81. Type species (by original designation): *Amussium caducum* E. A. Smith, 1885; Recent, W of Luzon, Philippines.

Luteamussium Oyama, 1951: 82. Type species (by original designation): *Amussium sibogai* Dautzenberg & Bavay, 1904; Recent, Bali Sea, Indonesia.

Propeamussium alcocki (E. A. Smith, 1894)
Plate 1, figs. 1–6

Amussium alcocki E. A. Smith, 1894: 172, pl. 5, figs. 15–16; Alcock & Anderson, 1897: pl. 2, figs. 3, 3a; Alcock, 1902: 282, fig. 79; E. A. Smith, 1906: 255; Thiele & Jaeckel, 1931: 8; Winckworth, 1940: 26.

Propeamussium alcocki (E. A. Smith). Abbott & Dance, 1982: 303, fig.; Dijkstra, 1995: 5, figs. 1–4, 133–137.

Type data: Lectotype (Dijkstra, 1995) ZSI 6154/9; 3 paralectotypes, BMNH 94.9.11.1, NMW 1955.158.785, ZMUC, "Investigator" stn 105, 15°02'N, 72°34'E, Laccadive Sea, alive, 1353 m.

Other material examined: NORFOLK ISLAND: P15, 30°10.7'S, 167°44.2'E, 952–949 m (NZOI, 1 pr).

Distribution: Northern Indian Ocean, Coral Sea, New Caledonia, Loyalty Islands, and Norfolk Island; 650–1469 m, living at 760–1353 m.
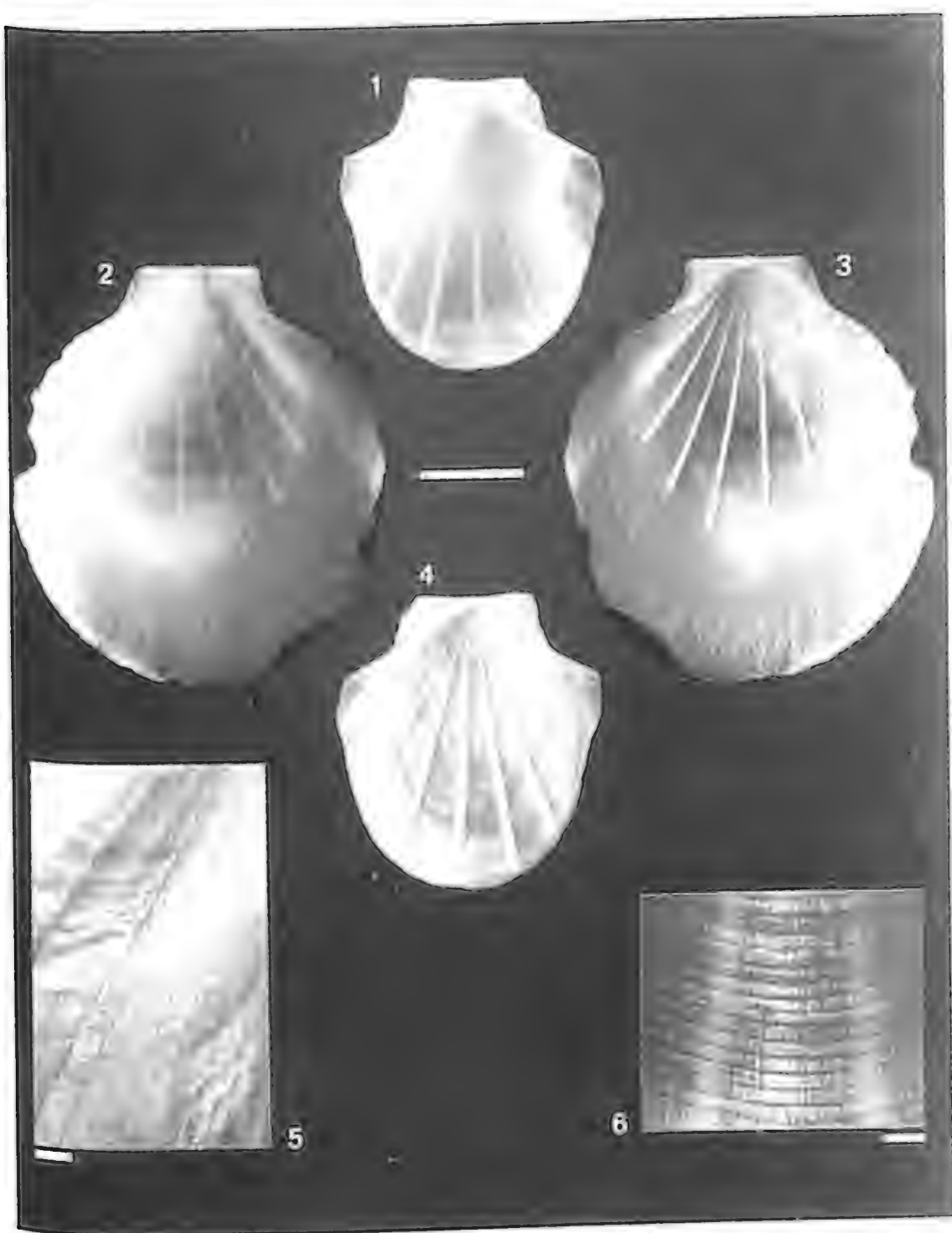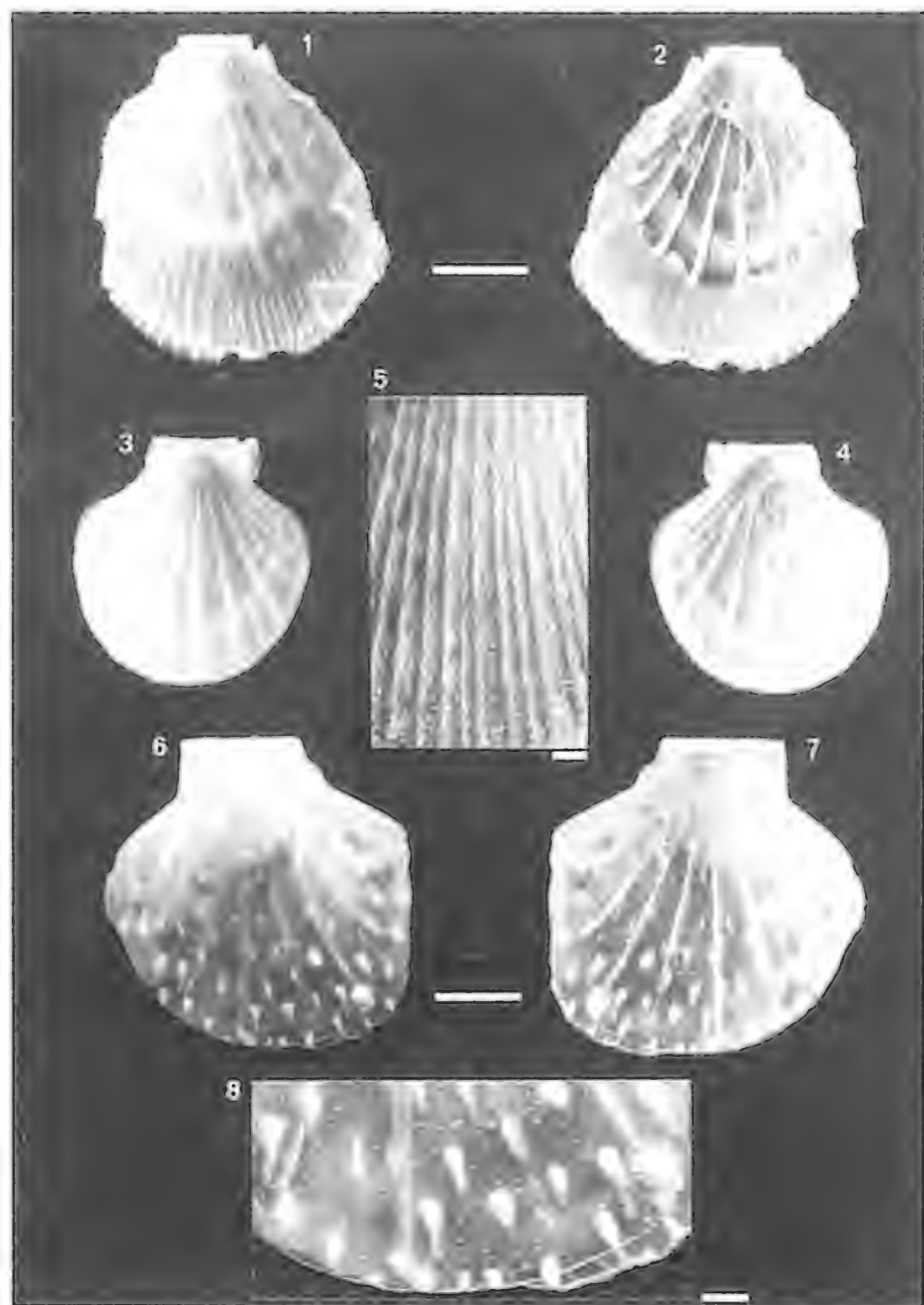
Plate 1.

Figures 1–6. *Propeamussium alcocki* (E.A. Smith, 1894), Norfolk Island, 949–952 m, NZOI. Figs. 1–4 (scale = 10 mm), figs. 5–6 (scale = 1 mm). Fig. 1. Right valve, exterior. Fig. 2. Left valve, exterior. Fig. 3. Left valve, interior. Fig. 4. Right valve, interior. Fig. 5. Left valve, exterior, postero-marginal area. Fig. 6. Right valve, exterior, central area.

Remarks: The present specimen is similar to the type material. Immature specimens lack the close-spaced concentric lamellae near the ventral margin of the left valve. *Propeamussium watsoni* (E. A. Smith, 1885) is somewhat similar to *P. alcocki*, and differs from the present species by having a more orbicular shape, concentric and radial sculpture on left valve (*P. alcocki* smooth or concentric growth lines), and more prominent concentric lamellae on the right valve.

Propeamussium maorium (Dell, 1956)
Plate 2, figs. 1–5

Parvamussium maorium Dell, 1956: 20, figs. 30–31; Powell, 1979: 381, figs. 93.1–2; Rombouts, 1991: 69.

Parvamussium maorum [sic] Dell, 1962: 75; 1963: 206.

Propeamussium maorium (Dell). Dijkstra, 1995: 10, figs. 11–14.

Type data: Holotype, NMNZ M.9171, "Alert" stn 54–17, Canyon A, ENE of Taiaroa Head, New Zealand, 476–640 m.

Other material examined: NORFOLK ISLAND: AUZ021, 28°53'S, 168°07'E, NE of Norfolk I., 732–567 m, R.N.Z.F.A. "Tui" (NMNZ M.224633, 1 v). KERMADEC ISLANDS: NMNZ stn BS442, 29°16.5'S, 177°49.5'W, SE of Chanter Is., Raoul I., alive, 512–549 m, R.V. "Acheron" (NMNZ M.225611, 6 pr & 12 v).

Distribution: Coral Sea, Loyalty Islands, Norfolk Island, Kermadec Islands, and New Zealand; 476–732 m, living at 512–549 m.

Remarks: *Propeamussium maorium* is most similar to *P. investigatoris* (E. A. Smith, 1906) from the southeastern Arabian Sea, but differs by having the left valve entirely smooth instead of sculptured with radial and concentric striae on the early part. Moreover, the radial costae are somewhat more prominent in *P. maorium*. Another similar species is *Propeamussium jeffreysii* (E. A. Smith, 1885) from the Philippines, which differs by having fine, somewhat cancellate sculpture on the left valve from the umbo to the central part of the disc, and in that some mature specimens have concentric lamellae near the periphery. We are unable to distinguish specimens from the Kermadecs and Norfolk Island from the type and other New Zealand specimens of *P. maorium*.

## *Propeamussium rubrotinctum* (Oyama, 1951)
Plate 2, figs. 6–8

Parvamussium (Parvamussium) rubrotinctum Oyama, 1951: 81, pl. 13, figs. 8–10.

Propeamussium (Propeamussium) stella Wang, 1984: 600, 602, pl. 1, figs. 11–14.

Propeamussium rubrotinctum (Oyama). Hayami, 1988a: 80; Dijkstra, 1995: 13, figs. 23–26.

Type data: *Propeamussium rubrotinctum*: Type material probably in the private collection of Dr K. Oyama at Toba, Japan (I. Hayami, pers. comm.). *Propeamussium stella*: Holotype IOAS M25778; paratype, IOAS M25779, South China Sea, 19°00'N, 112°05'E, 290 m.

Plate 2.   Figures 1–5. *Propeamussium maorium* (Dell, 1956), Kermadec Islands, 512–549 m, NMNZ M.225611. Figs. 1–4 (scale = 5 mm), fig. 5 (scale = 1 mm). Fig. 1. Left valve, exterior. Fig. 2. Left valve, interior. Fig. 3. Right valve, exterior. Fig. 4. Right valve, interior. Fig. 5. Left valve, exterior, ventral area. Figures 6–8. *Propeamussium rubrotinctum* (Oyama, 1951), Norfolk Island, 280–350 m, NZOI. Figs. 6–7 (scale = 5 mm), fig. 8 (scale = 1 mm). Fig. 6. Left valve, exterior. Fig. 7. Left valve, interior. Fig. 8. Left valve, exterior, ventral area.
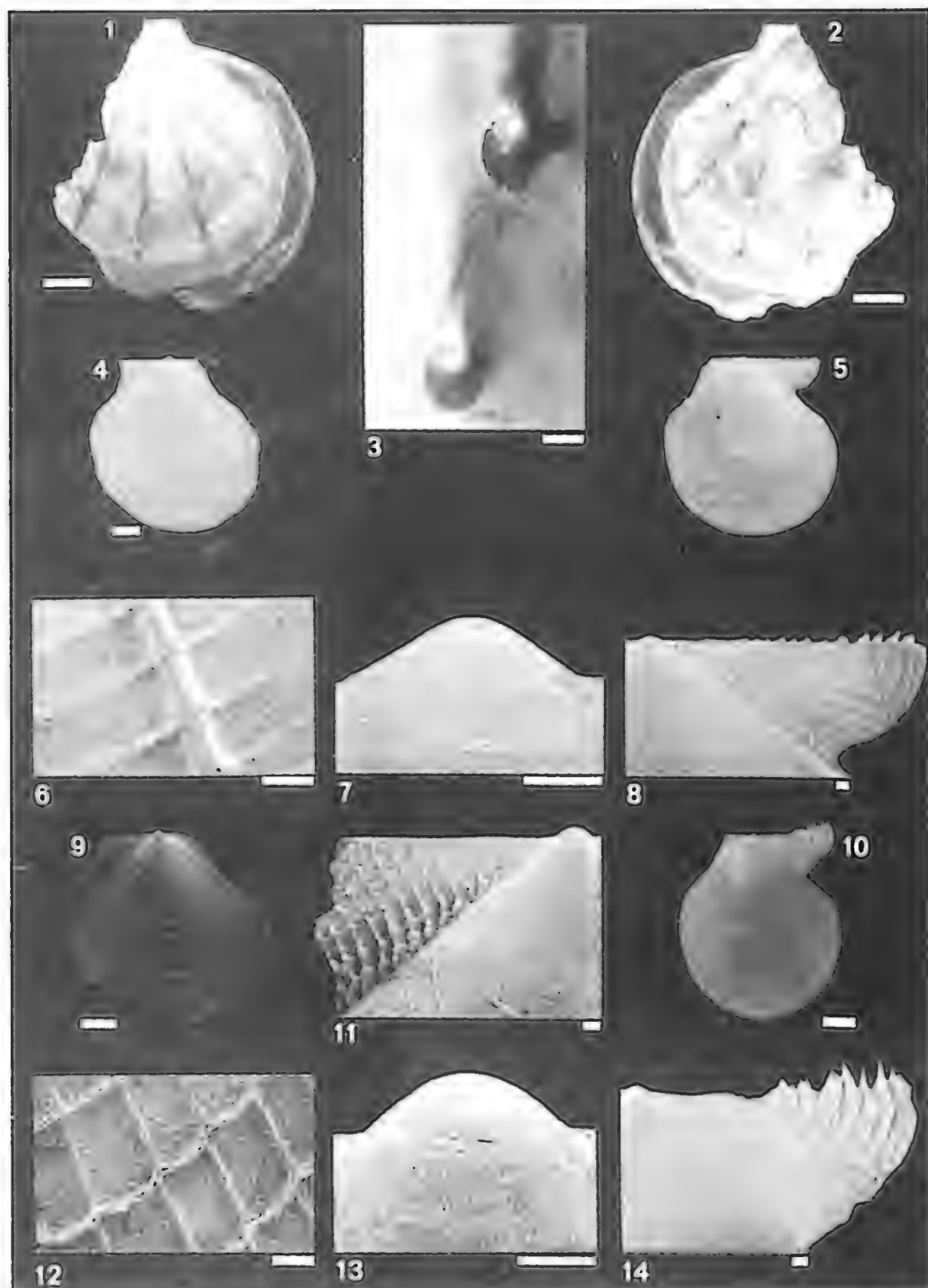
Other material examined: NORFOLK ISLAND: I86, 29°29.9'– 29°29.7'S, 167°50.5'–167°50.4'E, 280–350 m (NZOI, 6 v).

Distribution: Southern Japan, South China Sea, New Caledonia, Loyalty Islands, and Norfolk Island; 280–610 m, living at 380–490 m.

Remarks: *Propeamussium steindachneri* (Sturany, 1901) from the Red Sea and the Gulf of Oman is somewhat similar to *P. rubrotinctum*, but attains a smaller size (approximately 14mm instead of 20mm) and has fewer internal costae (8 instead of 10). Shell characters of *P. stella* Wang, 1984 from the South China Sea and of the present species are identical, although the coloration is somewhat different (orange instead of white maculations).

Propeamussium sibogai (Dautzenberg & Bavay, 1904)
Plate 3, figs. 1–3

Amussium sibogai Dautzenberg & Bavay, 1904: 207–211, figs. 1–4; 1912: 31, pl. 28, figs. 1–4.

Luteamussium sibogai (Dautzenberg & Bavay). Oyama, 1951: 82, text fig. 1; Kira, 1962: 138, pl. 49, fig. 14.

Propeamussium sibogai (Dautzenberg & Bavay). Knudsen, 1967: 272–273, pl. 1, figs. 23–24; Abbott & Dance, 1982: 303, fig.; Wang, 1984: 599, text fig. 1, figs. 1–2; Hayami, 1988: 479, 480, figs. 2.4a–d; Okutani, Tagawa & Horikawa, 1989: 59, fig.; Dijkstra, 1990a: 9; 1995: 15, figs. 19–22; Rombouts, 1991: 66, pl. 27, figs. 1–1a; Lamprell & Whitehead, 1992: text unpag, pl. 6, fig. 34.

Amussium cf. *sibogai* (Dautzenberg & Bavay). Barnard, 1969: 655, pl. 1, figs. a–d.

Propeamussium (Luteamussium) sibogai (Dautzenberg & Bavay). Koyama, Yamamoto, Toki & Minato, 1981: 62.

Luteamusium sibogae [sic] (Dautzenberg & Bavay). Kosuge, 1985: 59, pl. 23, fig. 12.

Type data: Holotype ZMA Moll. 3.04.001, "Siboga" stn 12, 7°15'S, 115°15.6'E, Bali Sea, Indonesia, alive, 289 m.

Other material examined: KERMADEC ISLANDS: AUZ114, off Curtis I., c. 300 m, R.N.Z.F.A. "Tui" (NMNZ M.223545, 1 v); P948, 24°17.70'S, 178°50.10'W, 589 m (NZOI, 1 valve).

Distribution: South Africa, Japan, Philippines, Indonesia, Timor Sea, New Caledonia and Loyalty Islands, and Kermadec Islands; 183–710 m, living at 430–575 m.

Remarks: The present specimens resemble the type specimen of *P. sibogai*, but differ by being semi-transparent with fewer yellowish radial stripes, and by having smaller brownish internal costae.

Plate 3. Figures 1–3. *Propeamussium sibogai* (Dautzenberg & Bavay, 1904), Kermadec Islands, c. 300 m, NMNZ M.223545. Figs. 1–2 (scale = 10 mm), fig. 3 (scale = 1 mm). Fig. 1. Left valve, exterior. Fig. 2. Left valve, interior. Fig. 3. Left valve, internal pustules. Figures 4–8. *Parvamussium cristatellum* (Dautzenberg & Bavay, 1912), Kermadec Islands, 256–348 m, NMNZ M.225398. Figs. 4–5 (scale = 1 mm), figs. 6–8 (scale = 100 µm). Fig. 4. Left valve, exterior. Fig. 5. Right valve, exterior. Fig. 6. Left valve, exterior, microsculpture, postero-ventral area. Fig. 7. Left valve, prodissoconch. Fig. 8. Right valve, exterior, anterior auricle. Figures 9–14. *Parvamussium retiaculum* Dijkstra, 1955, Norfolk Island, 538–545 m, NMNZ M.225311. Figs. 9–10 (scale = 1 mm), figs. 11–14 (scale = 100 µm). Fig. 9. Left valve, exterior. Fig. 10. Right valve, exterior. Fig. 11. Left valve, exterior, anterior auricle. Fig. 12. Left valve, exterior, microsculpture, postero-ventral area. Fig. 13. Left valve, prodissoconch. Fig. 14. Right valve, exterior, anterior auricle.

Genus *Parvamussium* Sacco, 1897

Parvamussium Sacco, 1897: 102. Type species (by original designation): *Pecten (Pleuronectes) duodecimlamellatus* Bronn, 1832; Upper Miocene, Tabbiano, northern Italy.

Variamussium Sacco, 1897: 102. Type species (by original designation): *Amussium cancellatum* E. A. Smith, 1885; Recent, off Bermuda, W Atlantic.

Ctenamusium Iredale, 1929: 164. Type species (by original designation): *Amusium thetidis* Hedley, 1902; Recent, off Port Kembla, New South Wales, Australia.

Glyptamusium Iredale, 1939: 370. Type species (by original designation): *Amussium torresi* E. A. Smith, 1885; Recent, E of Cape York, Queensland, Australia.

Squamamussium Oyama, 1944: 245. Type species (by original designation): *Amussium squamigerum* E. A. Smith, 1885; Recent, off E Puerto Rico, West Indies.

Polynemamussium Habe, 1951: 72. Type species (by original designation): *Pecten intuscostatus* Yokoyama, 1920; Pleistocene, Kami-Miyata, Miura City, Kanagawa Prefecture, Japan.

Remarks: As currently defined (Schein-Fatton, 1988; Schein, 1989; Hayami & Kase, 1993) *Parvamussium* differs from *Propeamussium* in having unequal instead of equal auricles, in lacking of disc gapes (anterior and posterior) and in having a well-developed byssal notch, while the internal costae commence at a late stage of growth. *Parvamussium* species attain smaller size than *Propeamussium* species (length 5–20 mm, and 15–85 mm respectively).

Parvamussium cristatellum (Dautzenberg & Bavay, 1912)
Plate 3, figs. 4–8. Plate 4, figs. 1–2

Pecten (Amussium) cristatum Bavay, 1905: 187, pl. 17, figs. 2a–c (not Bronn, 1831).

Amussium cristatellum Dautzenberg & Bavay, 1912: 36, pl. 28, figs. 5–8 (new name for *Pecten (Amussium) cristatum* Bavay, not Bronn).

Amussium texturatum (Dautzenberg & Bavay). Barnard, 1964: 432 (not *Amussium texturatum* Dautzenberg & Bavay, 1912).

Propeamussium (Parvamussium) cristatellum (Dautzenberg & Bavay). Dijkstra, 1990a: 9.

Parvamussium cristatellum (Dautzenberg & Bavay). Rombouts, 1991: 67.

Type data: 3 Syntypes ZSI M3360/1, "Masandam insulam" (Masandam Islands, Andaman Islands), depth unknown.

Other material examined: KERMADEC ISLANDS: BS439, 29°15.3'S, 177°49.3'W, E of Chanter Is., Raoul I., 256–348 m, R.V. "Acheron" (NMNZ M.225398, 49 v); BS441, 29°15.5'S, 177°50'W, E of Chanter Is., Raoul I., 366–402 m, R.V. "Acheron" (NMNZ M.225529, 30 v); BS442, 29°16.5'S, 177°49.5'W, SE of Chanter Is., Raoul I., 512–549 m, R.V. "Acheron" (NMNZ M.225616, 1 v).

Distribution: Southeastern Africa, Andaman Islands, Indonesian Archipelago and Kermadec Islands, 74–549 m, living at 510 m.

Remarks: The present specimens differ slightly from the type material in having more prominent concentric lamellae on the left valve, and weaker, irregularly spaced radial costae.
    A closely similar species is *Parvamussium thetidis* (Hedley, 1902) from southern Australia, which differs in having more closely spaced concentric lamellae on the left valve, weaker radial costae, and stronger internal costae, which commence at an earlier stage of growth.
    Parvamussium siebenrocki (Sturany, 1901) from the northwestern Indian Ocean is also closely

similar to *P. cristatellum*, but slightly differs in sculpture (less prominent) on the left valve and internal ribbing (more rudimentary intercostal ribs). It might be a senior synonym of the present species, as already suggested by Dijkstra (1991: 14). *Parvamussium formosum* (Melvill in Melvill & Standen, 1907) also from the northwestern Indian Ocean differs from *P. cristatellum* in having a very weak sculpture on the left valve (to nearly smooth) and some more internal costae.

South African specimens identified as *Parvamussium texturatum* by Barnard (1964), are indistinguishable from the type material and other specimens of *P. cristatellum*.

Parvamussium retiaculum Dijkstra, 1995
Plate 3, figs. 9–14. Plate 4, figs. 3–4

Parvamussium retiaculum Dijkstra, 1995: 20, figs. 35–38.

Type data: Holotype MNHN, BIOCAL stn DW51, 23°05'S, 167°45'E, southern New Caledonia, alive, 680–700 m.

Other material examined: NORFOLK ISLAND: AUZ 09, 30°46'S, 173°50'E, Kiwi Seamount, northern Three Kings Rise, 538–545 m, R.N.Z.F.A. "Tui" (NMNZ M.225311, 5 v). KERMADEC ISLANDS: BS442, 29°16.5'S, 177°49.5'W, SE of Chanter Is., Raoul I., 512–549 m, R.V. "Acheron" (NMNZ M.225615, 1 v).

Distribution: Southern New Caledonia, SE of Norfolk Island and off Raoul Island, Kermadec Islands; 512–775 m, living at 680–700 m.

Remarks: The present material is similar to the type specimens of *P. retiaculum* from southern New Caledonia, although one specimen has slightly more closely spaced concentric lamellae on the left valve. *P. retiaculum* somewhat resembles *Parvamussium multiliratum* Dijkstra, 1995 from southern New Caledonia, but is less orbicular in shape with larger auricles, and has fewer internal costae that are more irregular in size.

Parvamussium squalidulum Dijkstra, 1995
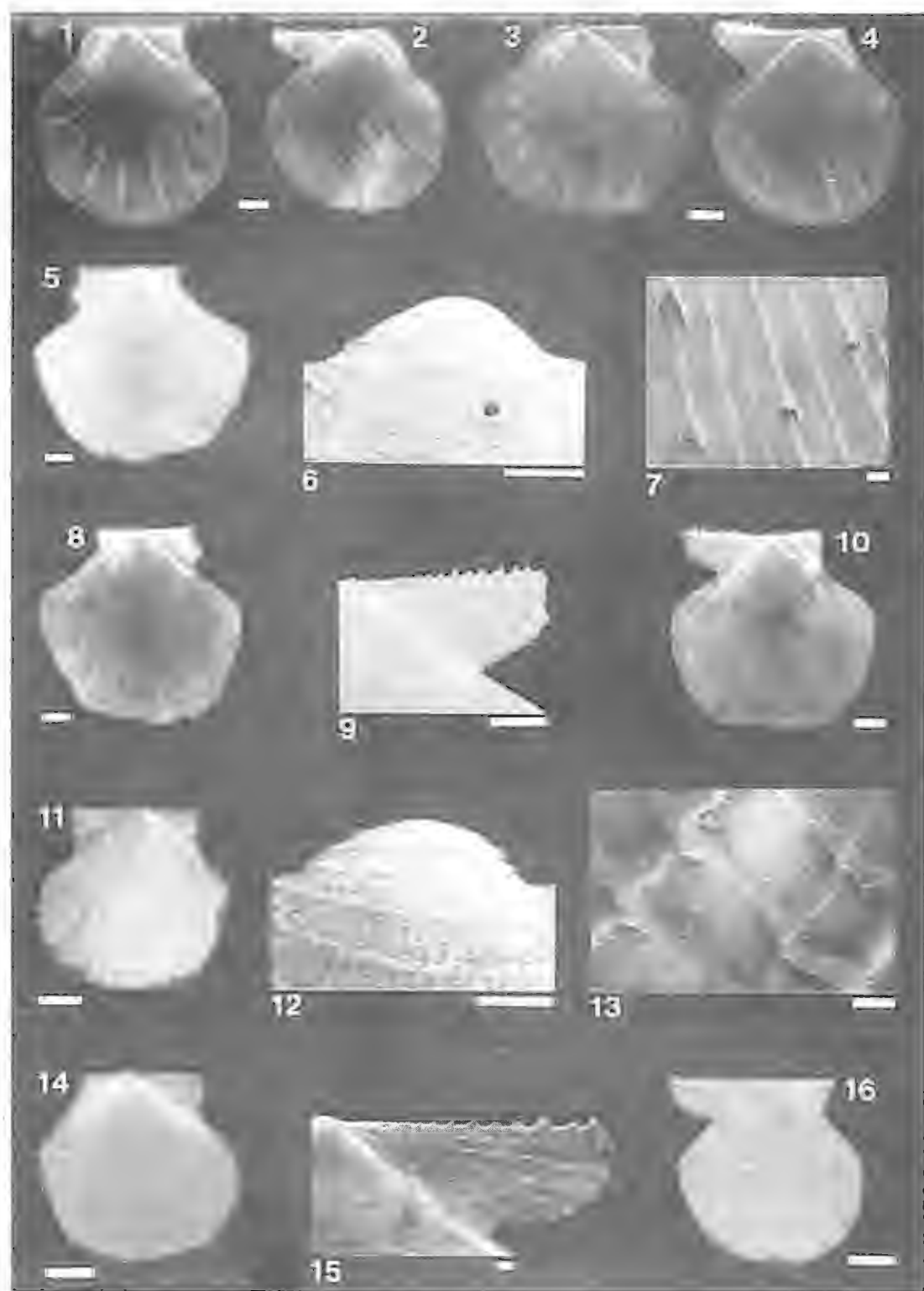Plate 4, figs. 5–10

Parvamussium squalidulum Dijkstra, 1995: 24, figs. 47–50.

Type data: Holotype, MNHN, MUSORSTOM 5 stn DW277, 24°11'S, 159°35'E, Kelso Banc, Coral Sea, alive, 270 m.

Other material examined: KERMADEC ISLANDS: K825, 28°47.8'S, 177°47.8'W, 145 m (NZOI, 12 v); BS438, 29°14.7'S, 177°49.4'W, SE of Nugent I., Raoul I., 146–165 m, R.V. "Acheron" (NMNZ M.225679, 1 v); AUZ113, off Curtis I., alive, 302 m, R.N.Z.F.A. "Tui" (NMNZ M.224639, 1 pr + 3 v).

Distribution: Coral Sea, Loyalty Islands, Vanuatu, and Kermadec Islands; 146–610 m, living at 260–400 m.

Remarks: The Kermadec specimens are similar to the type material. The internal costae (6–12) are very variable in number and are irregularly distributed. A closely similar species is *Parvamussium sinense* (Wang, 1980) from the East China Sea, which has stronger, more closely spaced squamous radial costae on the left valve. It also has delicate concentric lamellae on the right valve, which are usually absent in *P. squalidulum*.

Parvamussium vesiculatum Dijkstra, 1995
Plate 4, figs. 11–16

Parvamussium vesiculatum Dijkstra, 1995: 29, figs. 59–62, 93–96.

Type data: Holotype, MNHN, BIOCAL stn DW44, 22°47'S, 167°14'E, SE New Caledonia, alive, 440–450 m.

Other material examined: NORFOLK ISLAND: AUZ036, 20°19'S, 168°07'E, off Norfolk Island, 110 m, R.N.Z.F.A. "Tui" (NMNZ M.224962, 1 v); AUZ037, 20°20'S, 168°09'E, off Norfolk Island, 201 m, R.N.Z.F.A. "Tui" (NMNZ M.224723, 18 v); AUZ040, 29°24'S, 168°10'E, off Norfolk Island, 326 m, R.N.Z.F.A. "Tui" (NMNZ M.224809, 2 v). NORFOLK RIDGE: CHALCAL 2 stn DW76, 23°41'S, 167°45'E, 470 m (MNHN, 2 pr); SMIB 3 stn DW22, 23°03'S, 167°19'E, 503 m (MNHN, 7 lv).

Distribution: Western and southern New Caledonia, and Norfolk Ridge; 260–700 m, living at 260–650 m.

Remarks: *Parvamussium vesiculatum* is most similar to *P. texturatum* (Dautzenberg & Bavay, 1912) from the Sulu Sea, which is slightly more orbicular with somewhat larger auricles, while the radial costae on the left valve are more prominent, and the concentric lirae are weaker and more widely spaced. *P. vesiculatum* is ornamented with nodules on the concentric lirae, whereas *P. texturatum* has more numerous scales. There are also differences in the internal costae, which are rudimentary and fewer in number in the present species, and well developed in *P. texturatum*.

Genus *Cyclochlamys* Finlay, 1926

Cyclochlamys Finlay, 1926: 452. Type species (by original designation): *Pecten transenna* Suter, 1913; Recent, off The Snares, New Zealand.

Chlamydella Iredale, 1929: 164, 188. Type species (by original designation): *Cyclopecten favus* Hedley, 1902; Recent, off New South Wales, Australia.

Remarks: Hertlein (1969: N353) treated *Cyclochlamys* Finlay, 1926 as a synonym of *Cyclopecten* Verrill, 1897 and considered the former genus as a nomen nullum (i.e. an unintentional alteration in spelling of *Cyclopecten*). Finlay (1926: 452), however, clearly differentiated *Cyclochlamys* from *Cyclopecten*.

Chlamydella Iredale, 1929 is a junior synonym of *Cyclochlamys* (Maxwell, 1988: 44). Both have a somewhat triangular prodissoconch, and a hexagonal microsculpture on the right valve. See also Hayami & Kase (1993: 61).

Plate 4. Figures 1–2. *Parvamussium cristatellum*, NMNZ M.225398, scale = 1 mm (see also pl. 3, figs. 4–5). Fig. 1. Left valve, interior. Fig. 2. Right valve, interior. Figures 3–4. *Parvamussium retiaculum* , NMNZ M.225311, scale = 1 mm (see also pl. 3, figs. 9–10). Fig. 3. Left valve, interior. Fig. 4. Right valve, interior. Figures 5–10. *Parvamussium squalidulum* Dijkstra, 1995, Kermadec Islands, 302 m, NMNZ M.224639. Figs. 5, 8–10 (scale = 1 mm), figs. 6–7 (scale = 100 μm). Fig. 5. Left valve, exterior. Fig. 6. Left valve, prodissoconch. Fig. 7. Left valve, exterior, microsculpture, postero-ventral area. Fig. 8. Left valve, interior. Fig. 9. Right valve, exterior, anterior auricle. Fig. 10. Right valve, interior. Figures 11–16. *Parvamussium vesiculatum* Dijkstra, 1995, Norfolk Island, 201 m, NMNZ M.224723. Figs. 11, 14, 16 (scale = 1 mm), figs. 12, 13, 15 (scale = 100 μm). Fig. 11. Left valve, exterior. Fig. 12. Left valve, prodissoconch. Fig. 13. Left valve, exterior, microsculpture, antero-ventral area. Fig. 14. Left valve, interior. Fig. 15. Right valve, exterior, anterior auricle. Fig. 16. Right valve, interior.
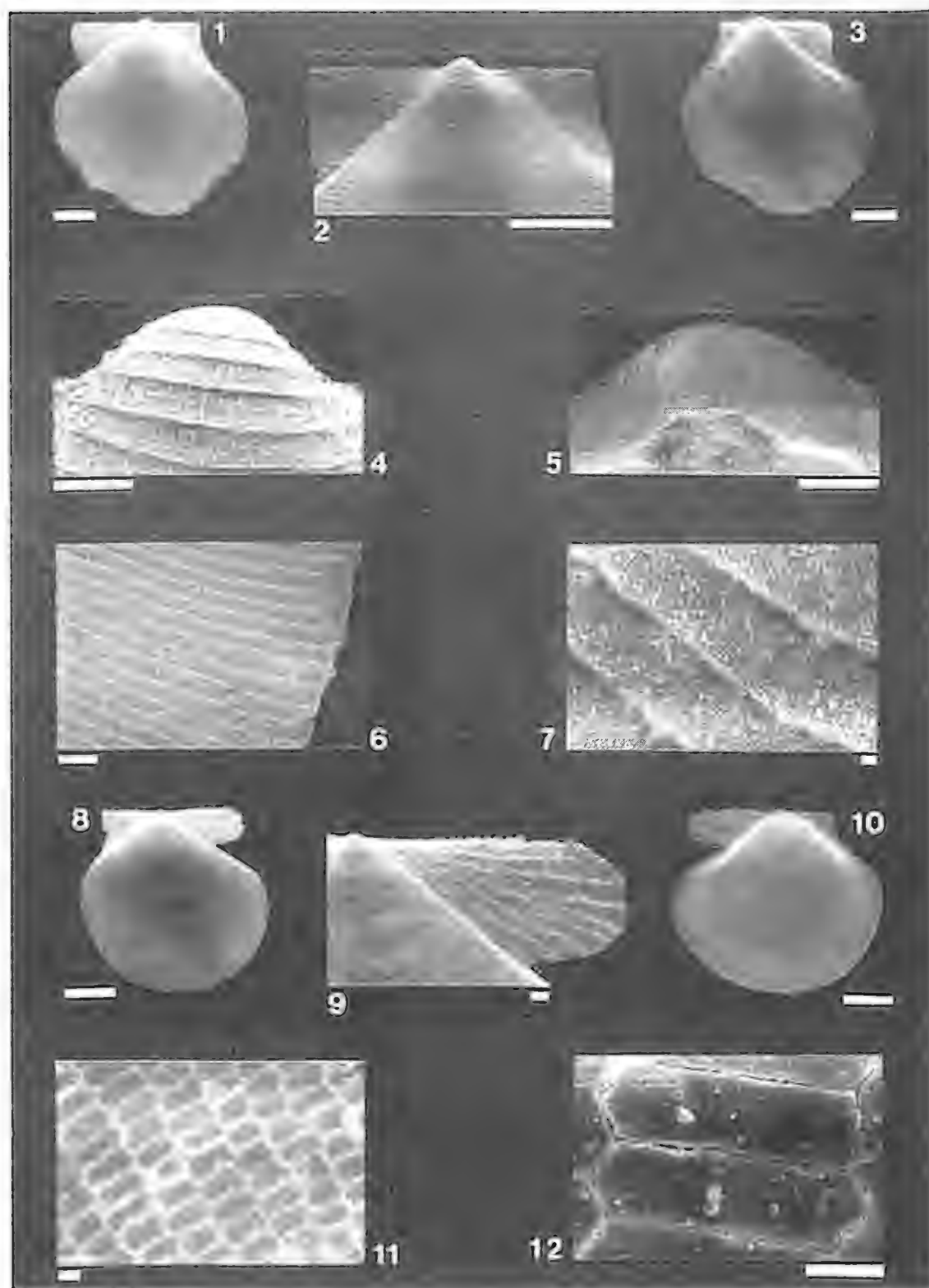
Several Australasian and Antarctic propeamussiids currently grouped in *Cyclopecten*, actually belong in *Cyclochlamys* (under study).

Cyclochlamys lemchei (Powell, 1958) (**Comb. nov.**)
Plate 5, figs. 1–12

Chlamydella favus lemchei Powell, 1958: 70–71, pl. 9 figs. 7–8.

Type data: Holotype (lv) ZMUC BIV–39; paratype (R.V.) ZMUC BIV–40, "Galathea" stn 674, 29°15'S, 177°5'W, off Raoul Island, Kermadec Islands, 75–85 m.

Other material examined: KERMADEC ISLANDS: AUZ113, off Curtis I., 302 m, R.N.Z.F.A. "Tui" (NMNZ M.224641, 2 v); BS296, off Hutchison Bluff, Raoul I., 84–113 m, R.V. "Acheron" (NMNZ M.222020, 25 v); BS434, 29°12.7'S, 177°56.1'W, NW of Fleetwood Bluff, Raoul I., 135 m, R.V. "Acheron" (NMNZ M.225444, many v); BS438, 29°14.7'S, 177°49.4'W, SE of Nugent I., Raoul I., alive, 146–165 m, R.V. "Acheron" (NMNZ M.225672, many pr); BS439, 29°15.3'S, 177°49.3'W, E of Chanter Is., Raoul I., 256–348 m, R.V. "Acheron" (NMNZ M.225399, 1 v); BS570, 29°14.73'S, 177°50.34'W, E of Dayrell I., Herald Is., alive, 135–146 m, R.V. "Acheron" (NMNZ M.226637, 38 pr); BS571, 29°18.8'S, 177°54.2'W, SE of D'Arcy Point, Raoul I., 219–274 m, R.V. "Acheron" (NMNZ M.226789, 12 v); BS572, 29°18.9'S, 177°56.4'W, SE of Smith Bluff, Raoul I., alive, 82–100 m, R.V. "Acheron" (NMNZ M.227157, many pr); BS573, 29°15'S, 177°50.9'W, Herald Is., between Dayrell and Chanter Is., 31–45 m, R.V. "Acheron" (NMNZ M.226973, 28 v); BS577, 29°17.2'S, 177°57.2'W, E end of Denham Bay, Raoul I., 27–29 m, R.V. "Acheron" (NMNZ M.226950, 1 v); BS579, 29°14'S, 177°59.28'W, NW of Hutchison Bluff, Raoul I., 38 m, R.V. "Acheron" (NMNZ M.226729, 16 v); 29°15'S, 177°52'E, Raoul I. (AMS C.300120, 4 v).

Distribution: Kermadec Islands, 27–348 m, living at 82–165 m.

Remarks: The present specimens are indistinguisable from the type material. Powell (1958: 71) compared *C. lemchei* with the southern Australian species *Cyclochlamys favus* (Hedley, 1902), and observed some differences: "the rapid obsolescence of the concentric lamellae in the left valve, with a compensating stronger development of the radial sculpture". *C. lemchei* differs, however, in attaining up to about 6 mm in length instead of about 3 mm, and is more orbicular in shape. Moreover, *C. lemchei* has a well developed colour pattern, while *C. favus* is colourless. The sculpture of the left valve of *C. favus* is highly variable, ranging from almost smooth to concentrically lamellate, radially lirate or reticulate. *C. lemchei* is constantly ornamented with diverging lirae. The hexagonal microsculpture of the right valve of *C. lemchei* is finer than in *C. favus*. Another closely allied species is *Cyclochlamys mestayerae* (Dell, 1956) from off northern New Zealand, which, however, lacks the sculpture on the left valve and is colourless.

Genus *Cyclopecten* Verrill, 1897

Cyclopecten Verrill, 1897: 70. Type species (by subsequent designation of Sykes, Smith & Crick, 1898): *Pecten pustulosus* Verrill, 1873; Recent, off Newfoundland, Canada.

Plate 5.   Figures 1–12. *Cyclochlamys lemchei* (Powell, 1958), Kermadec Islands, 135–146, NMNZ M.226637. Figs. 1–3, 8, 10 (scale = 1 mm), figs. 4–7, 9 (scale = 100 μm), figs. 11–12 (scale = 10 μm). Fig. 1. Left valve, exterior. Fig. 2. Left valve, exterior, dorsal area. Fig. 3. Left valve, interior. Fig. 4. Left valve, exterior, preradial stage. Fig. 5. Left valve, prodissoconch. Fig. 6. Left valve, exterior, antimarginal microsculpture, postero-ventral area. Fig. 7. Left valve, exterior, commarginal microsculpture, postero-ventral area. Fig. 8. Right valve, exterior. Fig. 9. Right valve, exterior, anterior auricle. Fig. 10. Right valve, interior. Fig. 11. Right valve, exterior, hexagonal microsculpture, antero-ventral area. Fig. 12. idem.
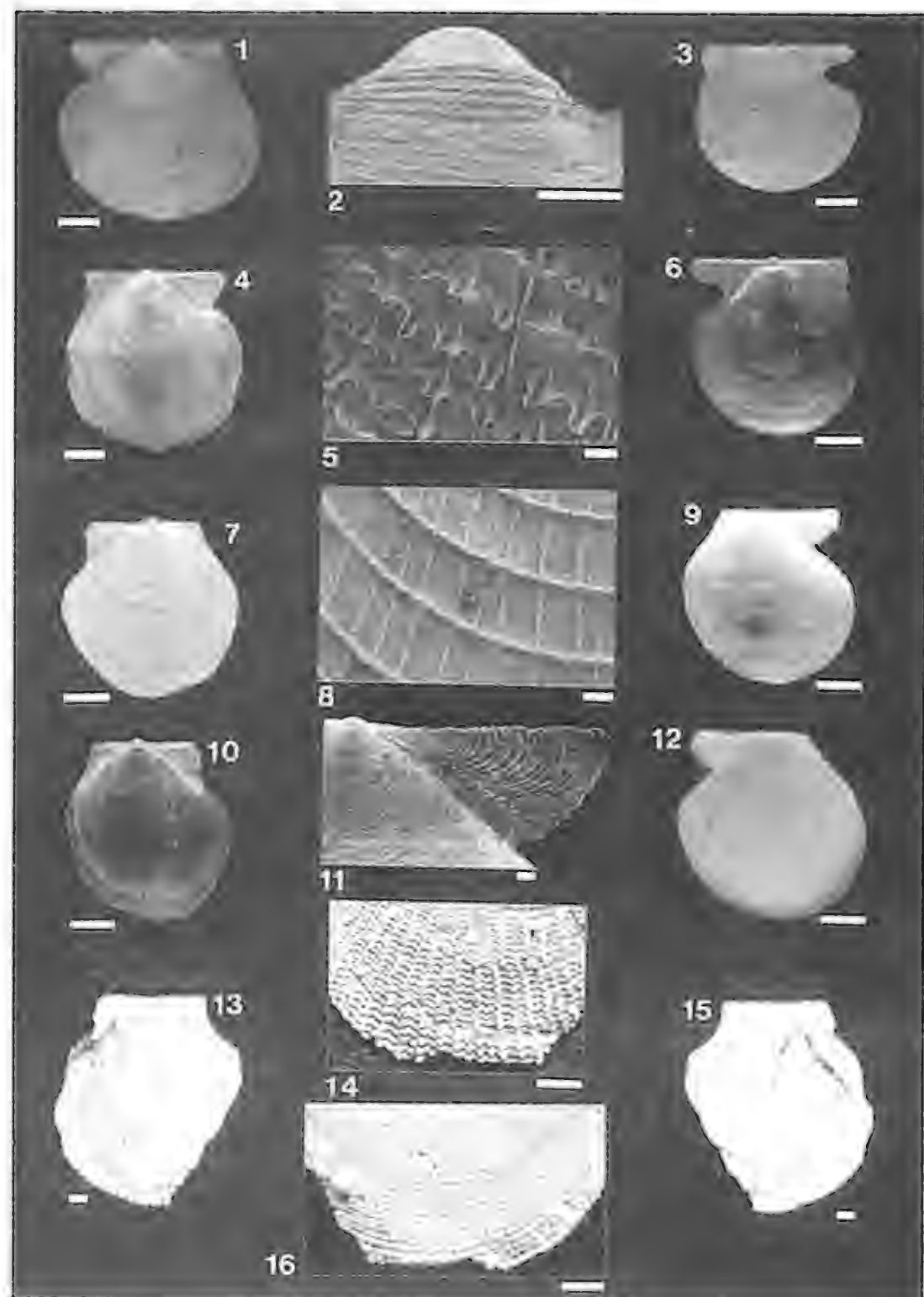
Xenamussium Oyama, 1944: 244. Type species (by original designation): *Pecten hoskynsi* Forbes, 1844; Recent, off Turkey, Mediterranean Sea.

Cyclopecten horridus Dijkstra, 1995
Plate 6, figs. 1–6

Cyclopecten horridus Dijkstra, 1995: 33, figs. 63–64, 98.

Type data: Holotype MNHN, MUSORSTOM 6 stn DW420, 20°29'S, 166°43'E, Loyalty Islands, alive, 600 m.

Other material examined: KERMADEC ISLANDS: K795, 33°02.6'S, 179°34.6'W, alive, 350 m (NZOI, 1 pr).

Distribution: Eastern New Caledonia, Loyalty Islands, and Kermadec Islands; 350–735 m, alive at 350–600 m.

Remarks: The present specimen is similar to the type material of *C. horridus*. Dijkstra (1995) compared two allied propeamussiids (*Parvamussium araneum* Dijkstra, 1991 from the Indonesian Archipelago, and *Parvamussium vidalense* (Barnard, 1964) from off South Africa) with the present one, both of which differ by having a few rudimentary internal costae.

Cyclopecten kapalae Dijkstra, 1990
Plate 6, figs. 7–12

Cyclopecten kapalae Dijkstra, 1990b: 29–32, figs. 1–5.

Type data: Holotype, AMS C.155831.1, 33°31'–33'S, 152°08'–07'E, off Sydney, New South Wales, 907–914 m, F.R.V. "Kapala" stn K80–20–08.

Other material examined: KERMADEC ISLANDS: BS442, 29°16.5'S, 177°49.5'W, SE of Chanter Is., Raoul I., alive, 512–549 m, R.V. "Acheron" (NMNZ M.225614, many pr).

Distribution: New South Wales and the Kermadec Islands; 512–914 m, alive at 512–549 m.

Remarks: The present specimens are similar to the type material, although the concentric lamellae on the left valve are slightly stronger and more widely spaced. Japanese specimens of the superficially similar species *C. bistriatus* (Dall, 1916) have finer reticulate sculpture on the left valve (Dijkstra, 1990b).

Plate 6. Figures 1–6. *Cyclopecten horridus* Dijkstra, 1995, Kermadec Islands, 600 m, NZOI. Figs. 1, 3, 4, 6 (scale = 1 mm), figs. 2, 5 (scale = 100 µm). Fig. 1. Left valve, exterior. Fig. 2. Left valve, prodissoconch. Fig. 3. Right valve, exterior. Fig. 4. Left valve, interior. Fig. 5. Left valve, exterior, commarginal sculpture and lamellae, antero-ventral area. Fig. 6. Right valve, interior. Figures 7–12. *Cyclopecten kapalae* Dijkstra, 1990, Kermadec Islands, 512–549 m, NMNZ M.225614. Figs. 7, 9, 10, 12 (scale = 1 mm), figs. 8, 11 (scale = 100 µm). Fig. 7. Left valve, exterior. Fig. 8. Left valve, exterior, com- and antimarginal microsculpture, antero-ventral area. Fig. 9. Right valve, exterior. Fig. 10. Left valve, interior. Fig. 11. Right valve, exterior, anterior auricle. Fig. 12. Right valve, interior. Figures 13–16. *Cyclopecten kermadecensis* (E.A. Smith, 1885), Kermadec Islands, 1189–1225 m, NMNZ M.222131. Figs. 13–16 (scale = 1 mm). Fig. 13. Left valve, exterior. Fig. 14. Left valve, exterior, microsculpture, ventral area. Fig. 15. Right valve, exterior. Fig. 16. Right valve, exterior, commarginal microsculpture, postero-ventral area.

Cyclopecten kermadecensis (E. A. Smith, 1885)

Plate 6, figs. 13–16

Pecten kermadecensis E. A. Smith, 1885: 302, pl. 21, figs. 7–7a.

Cyclopecten kermadecensis (E. A. Smith). Oliver, 1915: 553; Rombouts, 1991: 73.

Type data: Holotype BMNH 87.2.9.3279, "Challenger" stn 171, 28°33'S, 177°50'W, N of Kermadec Islands, 1097 m.

Other material examined: KERMADEC ISLANDS: BS312, 4 miles NNE of Herald Is., Raoul I., alive, 1189–1225 m, R.V. "Acheron" (NMNZ M.222131, 1 pr).

Distribution: Kermadec Islands, 1097–1225 m, living at 1189–1225 m.

Remarks: Smith (1885) stated that "Only two valves ... were obtained, and it is even possible that they do not both belong to one and the same species..." From examination of the two valves it is plausible that they represent a single individual, as the length of the hinge line of both valves (4.5 mm) is the same, and both valves fit together well. The fragile marginal apron of the right valve is broken off.

The present specimen is similar to the type valves.

Family Pectinidae Wilkes, 1810
[emend., Waller, 1978]

Subfamily Camptonectinae Habe, 1977

Genus *Delectopecten* Stewart, 1930

Delectopecten Stewart, 1930: 118. Type species (by original designation): *Pecten (Pseudamusium* [sic]) *vancouverensis* Whiteaves, 1893; Recent, Vancouver Island, British Columbia, Canada.

Remarks: Grau (1959: 38) and Beu (1970: 117) synonymised *Catillopecten* Iredale, 1939 with *Delectopecten*. Waller (1984: 214), however, treated *Catillopecten* as a distinct genus of Propeamussiidae. Schein (1989: 81) placed *Catillopecten* in Propeamussiinae Abbott, 1954 of Pectinidae and mentioned that *Bathypecten* Schein-Fatton, 1985 is closely related to *Catillopecten*. Recently Waller & Marincovich (1992: 219) placed *Delectopecten* in Camptonectinae Habe, 1977.

Delectopecten musorstomi Poutiers, 1981

Plate 8, figs. 1–6

Delectopecten musorstomi Poutiers, 1981: 331–332, pl. 1, figs. 2–3; Dijkstra, 1991: 26–27; 1995: 45, figs. 69–70.

Type data: Holotype MNHN, MUSORSTOM I stn 18, 13°57'N, 120°16.5'E, N of Lubang, Philippines, alive, 150–159 m.

Other material examined: NORFOLK ISLAND: AUZ037, 20°20'S, 168°09'E, off Norfolk I., 201 m, R.N.Z.F.A. "Tui" (NMNZ M.224686, 3 v).

Distribution: Philippines, Indonesian Archipelago, New Caledonia, and Norfolk Island; 130–495 m, living at 150–250 m.

Remarks: The present specimens are very similar to the holotype. There are fewer radial costae on the left valve than on the holotype (c. 12 instead of c. 20), but the number of costae is variable in material from Indonesia (12–18) (NNM). Moreover, the radial costae on the right valve are weaker

than in material from elsewhere. A closely allied species is *Delectopecten alcocki* (E. A. Smith, 1904), which attains much larger size (to c. 15 mm) and is ornamented with irregular scratches and (usually) delicate concentric lamellae. The radial costae are not squamous as in *D. musorstomi*. Another allied species is *Delectopecten fosterianus* (Powell, 1933) from New Zealand, which is also larger (to c. 20 mm), transparent, nearly smooth and lacks the characteristic diverging scratches.

Subfamily Hemipectinae Habe, 1977

Genus *Hemipecten* A. Adams & Reeve, 1849

Hemipecten A. Adams & Reeve, 1849: 133. Type species (by monotypy): *Hemipecten forbesianus* A. Adams & Reeve, 1849; Recent, Sulu Archipelago, Philippines.

Hemipecten forbesianus A. Adams & Reeve, 1849

Plate 7, figs. 1–6

Hemipecten forbesianus A. Adams & Reeve, 1849: 133, pl. 1, fig. 2; 1850: 72, pl. 20, figs. 1a–c, 2a–d; Waller, 1972: 256; Yonge, 1981: 23, 5 figs.; Dijkstra, 1990a: 5, pl. 2, figs. 11–12; Dijkstra et al., 1990: 3, fig.; Dijkstra, 1991: 24, fig.; Bernard, Cai & Morton, 1993: 51.

Pecten difformis Odhner, 1917: 15, pl. 1, figs. 4–5.

Cyclopecten (Hemipecten) forbesianus (A. Adams & Reeve). Rombouts, 1991: 79.

Type data: *Hemipecten forbesianus*: Lectotype (here designated) BMNH 1874.12.11.376, figured in Adams & Reeve (1849: pl. 1 fig. 2; 1850: pl. 20 figs 2a–d); paralectotype (Adams & Reeve, 1850: pl. 20 figs. 1a–c) not in type lot and not yet traced, Sulu Archipelago, c. 26 m. *Pecten difformis*: 6 Syntypes SMNH 1555, Pearl Bank, off Cape Jaubert, Western Australia.

Other material examined: NORFOLK ISLAND: I78, 29°06.8'S, 167°56.3'E, 6–28 m (NZOI, 1 pr).

Distribution: Southern Japan, Philippines, South China Sea, Indonesia, Western, northern and eastern Australia, Coral Sea, New Caledonia; 0–84m, living at 10–67 m.

Remarks: The present specimen is similar to the type material. Australian specimens (AMS, WAM) are very variable in shape (circular to elongate and oblique) probably caused by a constricted living position on the scleractinian coral *Turbinaria* (Yonge, 1981: 29). The shell characters of the immature type specimens of *P. difformis* from Western Australia are identical to that of *H. forbesianus*. The present specimen from Norfolk is exceptionally large (height 39.5 mm).

Subfamily Pectininae Wilkes, 1810

Tribe Pectinini Wilkes, 1810

Genus *Pecten* Müller, 1776

Pecten Müller, 1776: 248. Type species (by subsequent designation of Schmidt, 1818): *Ostrea maxima* Linnaeus, 1758; Recent, E Atlantic.

Deperetia von Teppner, 1922: 87, 259. Type species (by original designation): *Pecten cristatocostatus* Sacco, 1897; Miocene, Turin, Italy.

Heritschia von Teppner, 1922: 87, 264. Type species (by original designation): *Pecten aduncus* von Eichwald, 1830; Miocene, NW Ukraine.
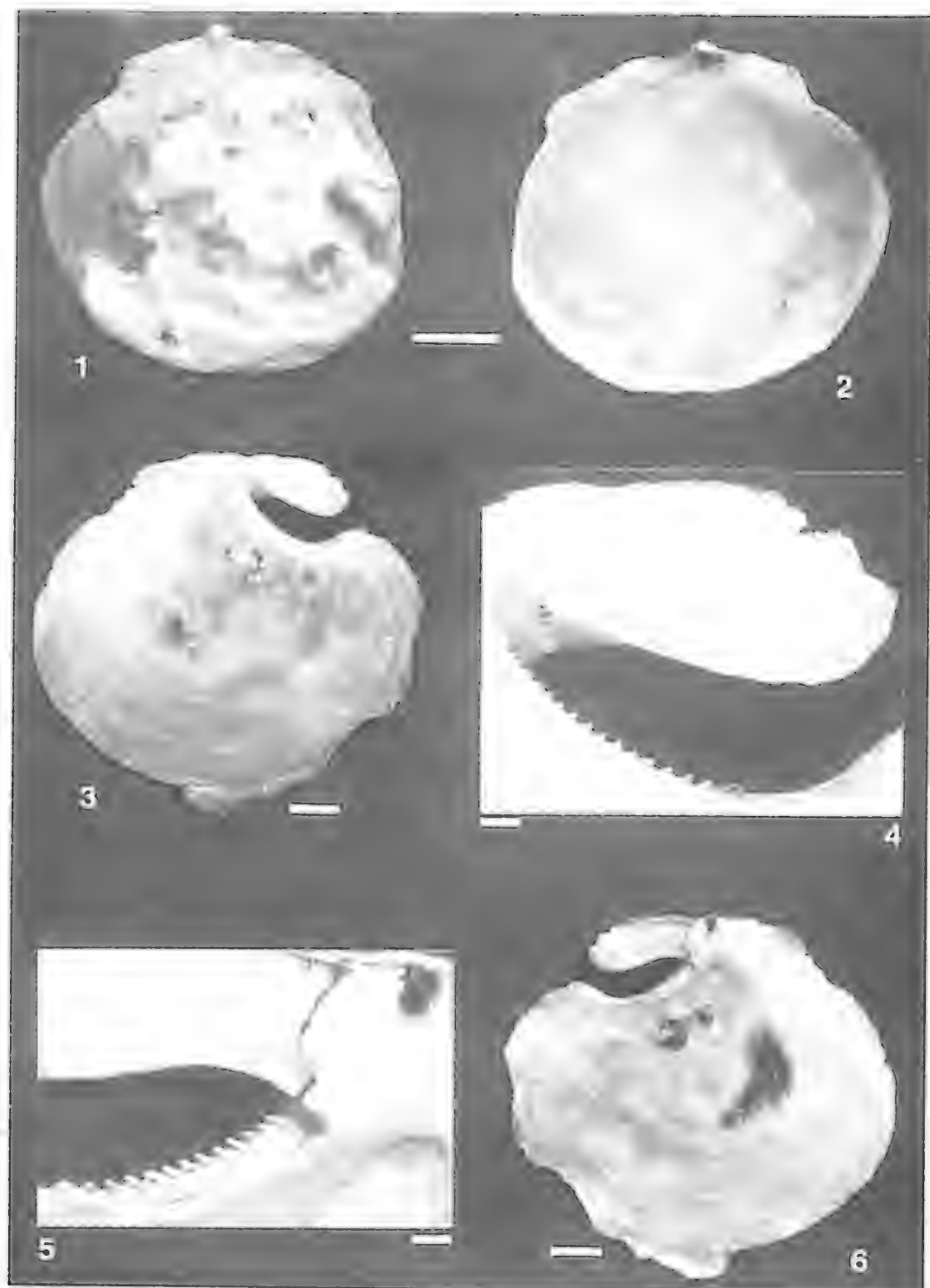
Jaworskia von Teppner, 1922: 87, 266. Type species (by original designation): *Pecten grandis* J. de
C. Sowerby, 1828; Pliocene, Suffolk Crag, Great Britain.

Notovola Finlay, 1926: 451. Type species (by original designation): *Pecten novaezelandiae* Reeve,
1852; Recent, New Zealand.

Pecten fumatus Reeve, 1852
Plate 13, figs. 1–2

Pecten medius Lamarck, 1819: 163; Hedley, 1902: 303; Pritchard & Gatliff, 1904: 261; Suter, 1913:
874 (partly); Iredale, 1924: 193; Finlay, 1926: 451; Cox, 1929: 203; Dijkstra, 1995 (not Bosc,
1802).

Pecten ziczac var. b Lamarck, 1819: 164; Deshayes in Lamarck, 1836: 131.

Pecten fuscus Sowerby II, 1842: 47, pl. 16, figs. 118–119 (not Bosc, 1802).

Pecten bifidus Menke, 1843: 35 (not Münster in Goldfuss, 1836); Philippi, 1845: 202, pl. 2, fig. 6.

Pecten lamarckii Chenu, 1843: 2, pl. 9, fig. 1 (not Defrance, 1825).

Pecten fumatus Reeve, 1852: spec. 32, pl. 7, fig. 32; Tate, 1887: 108; Fleming, 1951: 132; Rombouts,
1991: 50, pl. 18, fig. 8; Lamprell & Whitehead, 1992: no. 83, pl. 14, fig. 83.

Pecten modestus Reeve, 1852: spec. 41, pl. 11, fig. 41 (not Bosc, 1802).

Vola laticostata Angas, 1865: 656 (not Gray in Yate, 1835).

Vola fumata (Reeve). Angas, 1867: 933.

Pecten (Janira) fumatus Reeve. E. A. Smith, 1885: 307.

Pecten fumatus var. *albus* Tate, 1887: 113.

Pecten meridionalis Tate, 1887: 115 (not von Eichwald, 1865).

Notovola fumata (Reeve). Iredale, 1939: 365.

Notovola preissiana Iredale, 1949: 19.

Notovola meridionalis (Tate). Allan, 1950: 279, pl. 39, fig. 1.

Pecten jacobaeus byronensis Fleming, 1955: 108, fig. 1; 1957: 10, 16, 19, 25, 40, pl. 7, fig. 3
(holotype).

Pecten benedictus albus Tate. Fleming, 1957: 9, 16, 17, 19, 22, 33, pl. 2, fig. 1.

Pecten benedictus fumatus Reeve. Fleming, 1957: 9, 13, 16, 17, 19, 22, 28, 32, 33, 34, pl. 1, fig. 5
(lectotype).

Pecten jacobaeus meridionalis Tate. Fleming, 1957: 10, 12, 15, 16, 20, 22, 25, 32, 39, 40, pl. 7, fig.
4.

Pecten modestus Reeve. Fleming, 1957: 10, 16, 19, 36, 37, 38, pl. 7, figs. 5 (lectotype), 6
(paralectotype).

Plate 7.   Figures 1–6. *Hemipecten forbesianus* Adams & Reeve, 1849, Norfolk Island, 6–28 m, NZOI. Figs. 1–2 (scale
= 10 mm), figs. 3, 6 (scale = 5 mm), figs. 4–5 (scale = 1 mm). Fig. 1. Left valve, exterior. Fig. 2. Left valve,
interior. Fig. 3. Right valve, exterior. Fig. 4. Right valve, exterior, anterior auricle. Fig. 5. Right valve, interior,
ctenolium. Fig. 6. Right valve, interior.
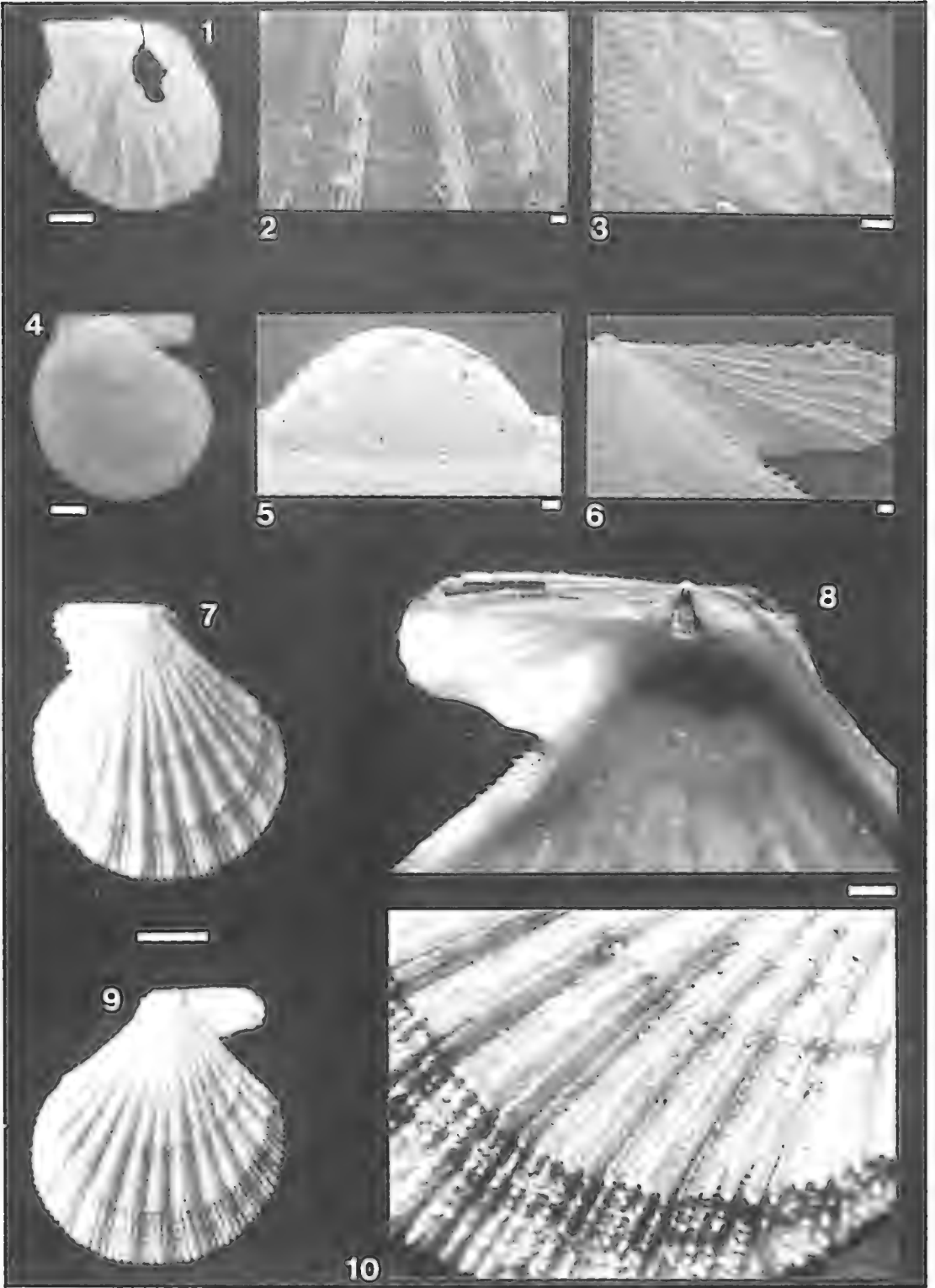
Notovola alba (Tate). Cotton, 1961: 96, fig. 81.

Pecten alba [sic] Tate. Macpherson & Gabriel, 1962: 300, fig. 341.

Notovola byronensis (Iredale). Garrard, 1969: 5.

Type data: *Pecten medius*: Lectotype (Dijkstra, 1995) and 3 paralectotypes MNHN, Australia (designated by Dijkstra, 1995). *Pecten fuscus*: 3 syntypes BMNH 1994.164, Moreton Bay, Queensland (Reeve, 1852). *Pecten fumatus*: 3 syntypes BMNH 1950.11.14.32–34, Sydney, New South Wales. *Pecten modestus*: Holotype UMZC 1382, Moreton Bay, Australia [sic] (= Swan River, Western Australia). *Pecten fumatus* var. *alba* [sic]: Holotype SAM D.8920, Port Lincoln, South Australia. *Notovola preissiana*: 5 syntypes AMS C.90371, Shark Bay, Western Australia. *Pecten jacobaeus byronensis*: Holotype AMS C.5243 and 2 paratypes (AMS C.170831), Byron Bay, New South Wales.

Other material examined: LORD HOWE ISLAND: NZOI stn P106, 31°27.7'S, 159°02.6'E, alive, 53 m (NZOI, 1 pr).

Distribution: Southern Queensland, New South Wales, Lord Howe I., Victoria, Tasmania, South Australia, and Western Australia as far north as Shark Bay; 0–80 m, living at 10–73 m.

Remarks: The present specimen is similar to the Queensland form of *P. fumatus*, although the radial costae of the left valve are somewhat more angular.

In a recent analysis of genetic variation in Australasian *Pecten*, Woodburn (1989) concluded that *P. meridionalis* Tate, 1887 (Tasmania) and *P. albus* Tate, 1887 (Victoria and South Australia) are synonyms of *P. fumatus* (Queensland and New South Wales), and that *P. novaezelandiae* and the Western Australian form (*N. preissiana* Iredale, 1949) are specifically distinct. The taxonomic status of *P. raoulensis* has yet to be determined.

A discussion of the Australian species of *Pecten* will be given elsewhere.

Pecten raoulensis Powell, 1958

Plate 13, figs. 3–4

Pecten medius Lamarck. Oliver, 1915: 553 (not Lamarck, 1819).

Pecten raoulensis Powell, 1958: 67, pl. 10, figs. 1–2.

Pecten novaezelandiae raoulensis Powell. Fleming, 1962: 184.

Type data: Holotype ZMUC, "Galathea" stn 674, 29°15'S, 177°57'W, off Raoul I., Kermadec Is., 75–85 m.

Other material examined: KERMADEC ISLANDS: Raoul I., dredged, R.S. Bell, 1913 (NMNZ, 1 pr, 1 v); BS 307, off and between Bell's Flat and Hutchison Bluff, Raoul I., alive, 110–146 m, R.V. "Acheron" (NMNZ, 1 pr); BS 308, between Bell's Flat and Hutchison Bluff, Raoul I., alive, 110–121

Plate 8. Figures 1–6. *Delectopecten musorstomi* Poutiers, 1981, Norfolk Island, 201 m, NMNZ M.224686. Figs. 1, 4 (scale = 1 mm), figs. 2, 3, 6 (scale = 100 µm), fig. 5 (10 µm). Fig. 1. Left valve, exterior. Fig. 2. Left valve, exterior, microsculpture, ventral area. Fig. 3. Left valve, exterior, antimarginal microsculpture, postero-ventral area. Fig. 4. Right valve, exterior. Fig. 5. Right valve, prodissoconch. Fig. 6. Right valve, exterior, anterior auricle. Figures 7–10. *Chlamys coruscans coruscans* (Hinds, 1845), Kermadec Islands, NMNZ M.202881. Figs. 7–9 (scale = 5 mm), figs. 8, 10 (scale = 1 mm). Fig. 7. Left valve, exterior. Fig. 8. Right valve, interior, dorsal area. Fig. 9. Right valve, exterior. Fig. 10. Right valve, exterior, costae with intermediate shagreen (reticulated) microsculpture, postero-ventral area.
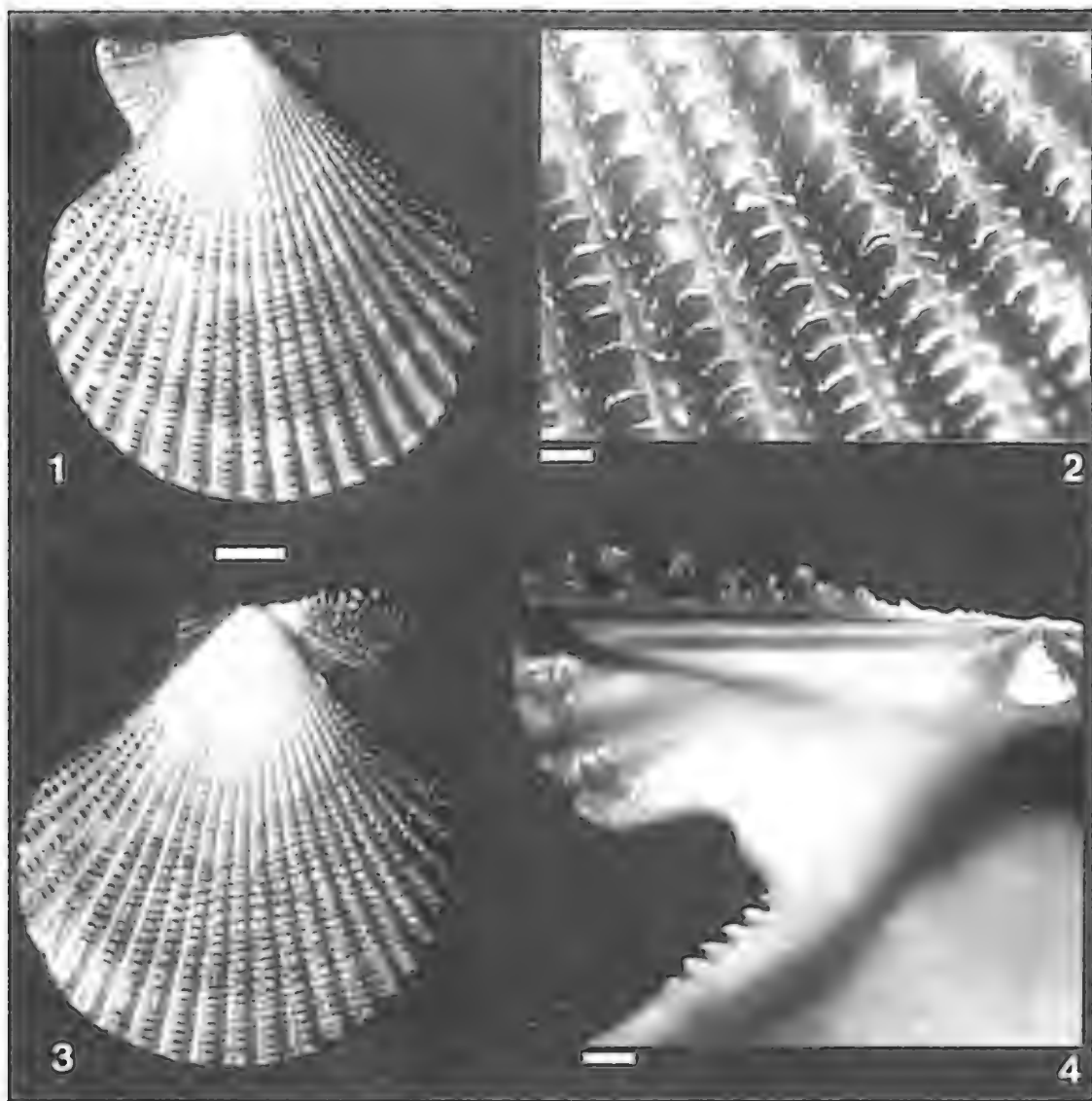
Plate 9.   Figures 1–4. *Mimachlamys senatoria* (Gmelin, 1791), Norfolk Island, 65 m, NZOI. Figs. 1, 3 (scale = 5 mm), figs. 2, 4 (scale = 1 mm). Fig. 1. Left valve, exterior. Fig. 2. Left valve, exterior, costae with lamellae, postero-ventral area. Fig. 3. Right valve, exterior. Fig. 4. Right valve, interior, anterior auricle, ctenolium.

m. R.V. "Acheron" (NMNZ, 1 pr), BS 296, off Hutchison Bluff, Raoul I., 84–113 m. R.V. "Acheron" (NMNZ, 6 v); K818, 29°13.31'S, 177°56.36'W, 95 m (NZOI, 1 v); K819, 29°13.24'S, 177°56.30'W, 100 m (NZOI, several v); K820, 29°13.30'S, 177°59.80'W, 95 m (NZOI, several v); 29°14.6'S, 177°52.6'W, off westside of Meyer I., 30 m (AIM AK 78573, 2 v); BS 567, 29°16'S, 177°52'W, East Anchorage, Raoul I., 42–47 m, R.V. "Acheron" (NMNZ, 2 v); BS 436, 29°18.5'S, 177°54.5'W, SE of D'Arcy Point, Raoul I., 44 m, R.V. "Acheron" (NMNZ, 1 v); K856, 30°33.5'S, 178°31.1'W, 125–130 m (NZOI, 1 v).

Distribution: Off Raoul Island, Kermadec Islands, 75–130 m, living at 110–146 m.

Remarks: *Pecten raoulensis* is similar to the New Zealand species *P. novaezelandiae* Reeve, 1852, and the Australian species *P. fumatus* Reeve, 1852, both of which are variable in sculpture, auricle size, valve convexity, colour and colour pattern. Specimens from depths greater than 50 m, including the holotype, have sculpture that falls within the range exhibited by both Recent *P. novaezelandiae* and *P. fumatus*. Specimens from shallower depths differ from Recent *P. novaezelandiae* in the greater strength and earlier appearance of the concentric lamellae, and in the greater strength of the radial sculpture in shells less than 20 mm in length. The latter specimens thus more closely resemble *P. fumatus* than *P. novaezelandiae*, especially specimens from Queensland. Both Kermadec forms, which are evidently conspecific, differ further from *P. novaezelandiae* in that the left valve extends further beyond the right valve and more strongly overhangs it, as in many specimens of *P. fumatus*. We conclude, therefore, that *P. raoulensis* is more closely related to *P. fumatus* than to *P. novaezelandiae*, which is contrary to the opinion of Fleming (1962), who considered it a geographic subspecies of *P. novaezelandiae*.

Genus *Amusium* Röding, 1798

Amusium Röding, 1798: 165. Type species (by subsequent designation of Herrmannsen, 1846): *Ostrea pleuronectes* Linnaeus, 1758; Recent, Indonesia.

Pleuronectia Swainson, 1840: 388. Type species (by monotypy): *Pleuronectia laevigata* Swainson, 1840 (= junior synonym of *Ostrea pleuronectes* Linnaeus, 1758); Recent, Indo-West Pacific.

Amusium balloti (Bernardi, 1861)

Pecten balloti Bernardi, 1861: 46–48, pl. 1, fig. 1; Lischke, 1869: 165.

Pecten (Amussium) balloti Bernardi. De Gregorio, 1898: 7–8, pl. 1, figs. 3–4, 7; pl. 4, fig. 4.

Amusium japonicum balloti (Bernardi). Habe, 1964a: 4–5, pl. 1, fig. 5; pl. 2, fig. 6; Abbott & Dance, 1982: 303, fig.; Waller, 1991: 18, 37, pl. 8, figs. 5, 8.

Amusium balloti (Bernardi). Iredale, 1939: 369; Wells & Bryce, 1988: 158, pl. 60, fig. 579; Dijkstra, 1988: 3–4, figs.; 1990a: 3, figs.; 1991: 25–26; Dijkstra et al., 1989: 24; Rombouts, 1991: 3–4, pl. 2, figs. 5–5a; Lamprell & Whitehead, 1992: text unpag., pl. 7, fig. 38.

Type data: 3 Syntypes MNHN, "Nova-Caledonia" (New Caledonia).

Other material examined: NORFOLK ISLAND: P18, 29°34.60'S, 168°03.00'E, 90 m (NZOI, 1 v); P38, 29°10.40'S, 167°55.80'E, 64 m (NZOI, 2 v).

Distribution: Southwestern, southeastern and eastern Australia, Coral Sea, New Caledonia and Norfolk Island; 0–84 m, living at 18–60 m.

Remarks: Habe (1964a) treated *Amusium balloti* as a subspecies of *A. japonicum*, noting that while both are very similar in shape, *A. balloti* has fewer internal costae and is reddish brown instead of deep red. *A. japonicum* has not been recorded from the Philippines or the Indonesian Archipelago and despite their similarity, there seems to be no sufficient reason to treat *A. balloti* as a geographic subspecies. Forms with intermediate characters are unknown. Wang's (1984) record of *A. balloti* from China could represent a local population of *A. japonicum*, perhaps *A. japonicum taiwanense* Dijkstra, 1988. The present specimens from Norfolk Island are mere fragments.

Tribe Decatopectinini Waller, 1986
Genus *Annachlamys* Iredale, 1939

Annachlamys Iredale, 1939: 358. Type species (by original designation): *Pecten leopardus* Reeve, 1853 (=junior synonym of *Pecten flabellatus* Lamarck, 1819); Recent, Australia.
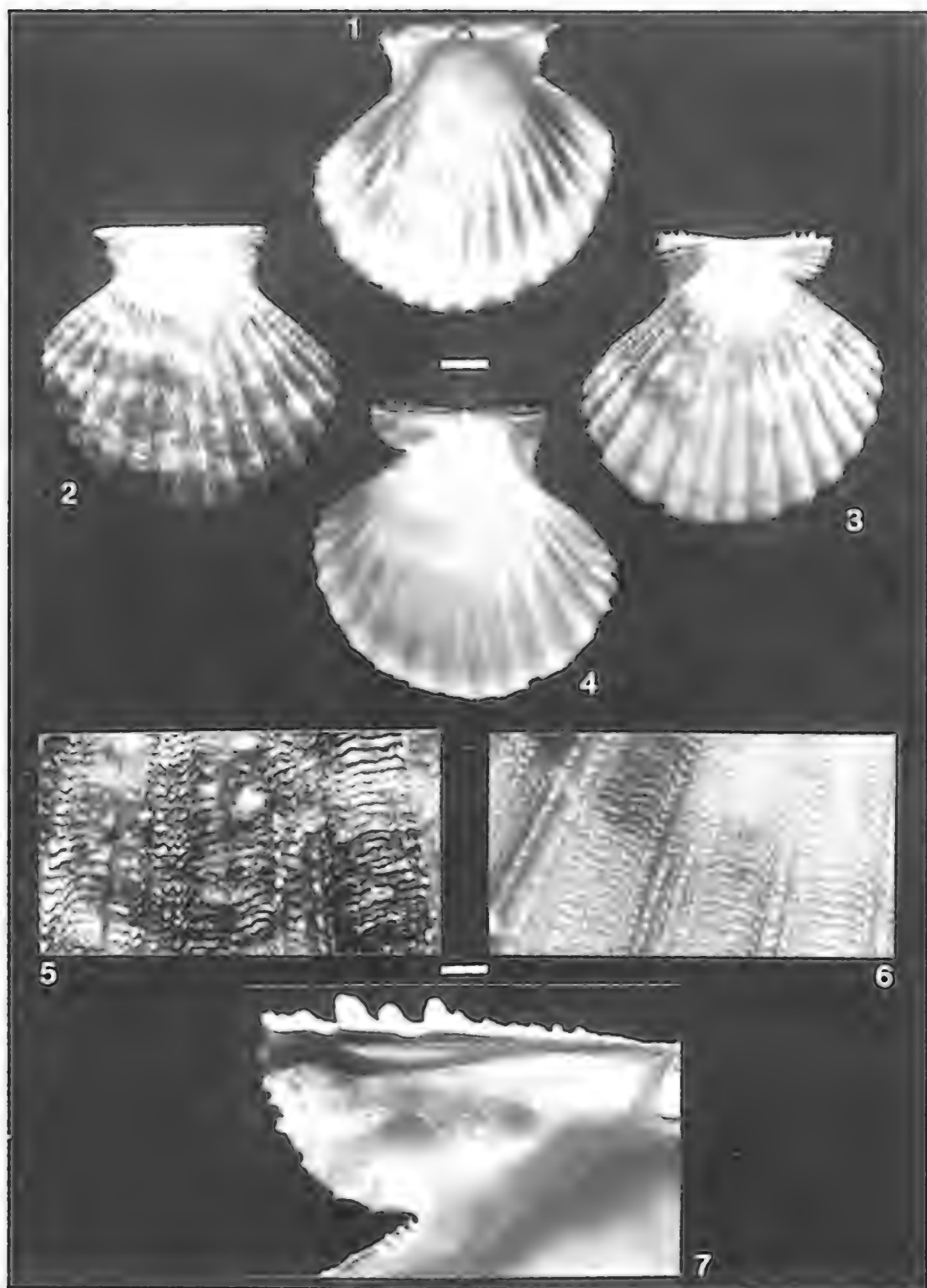
Annachlamys iredalei (Powell, 1958)

Plate 10, figs. 1–7

Aequipecten (Corymbichlamys) iredalei Powell, 1958: 68–69, pl. 11, figs. 1–2, text fig. 2.

Annachlamys iredalei (Powell). Dijkstra, 1989a: 19–20, figs.; 1990a: 8, 10, figs.; Dijkstra et al., 1989: 24; Lamprell & Whitehead, 1992: text unpag., pl. 11, fig. 64.

Corymbichlamys iredalei (Powell). Rombouts, 1991: 36, pl. 13, fig. 6.

Type data: Holotype ZMUC BIV–37, "Galathea" stn 675, 29°13.5'S, 177°57'W, off Raoul Island, Kermadec Islands, 58–60 m.

Other material examined: LORD HOWE ISLAND: H.M.A.S. "Kimbla" stn LH 5, 30°25.5'S, 159°5.6'E, 49–51 m (AMS C123839, 10 v); P114, 31°23.9'S, 159°05.4'E, 85–80 m (NZOI, 10 v); P105, 31°26.7'S, 159°07.2'E, 56 m (NZOI, 2 valves); P104, 31°30.0'S, 159°10.0'E, 75–72 m (NZOI, 1 v); P109, 31°30.2'S, 158°57.9'E, 69 m (NZOI, 1 valve); H.M.A.S. "Kimbla" stn LH 1, 31°34.9'S, 159°0.3'E, Lord Howe Rise, 73 m (AMS C123974, 5 v); H.M.A.S. "Kimbla" stn LH 4, 31°37.1'S, 159°13'E, 51–55 m (AMS C123844, many pr); P111, 31°37.6'S, 159°12.4'E, 57 m (NZOI, 2 v); H.M.A.S. "Kimbla" stn LH 2, 31°38.2'S, 159°3.6'E, 44 m (AMS C123718, many pr.); P99, 31°43.2'S, 159°12.4'E, 53–51 m (NZOI, 1 v); 31°45'S, 159°15'E, off Ball's Pyramid, 91–183 m (AMS C300228, 1 v); P82, 31°49.8'S, 159°19.7'E, 78–84 m (NZOI, 3 v). NORFOLK ISLAND: AUZ28, 28°54'S, 167°59'E, N of Norfolk I., 33 m, R.N.Z.F.A. "Tui" (NMNZ M.223562, 1 v); AUZ30, 28°59'S, 167°58'E, N of Norfolk I., 38 m, R.N.Z.F.A. "Tui" (NMNZ M.223567, 1 valve); I84, 29°07.8'S, 168°09.9'E, 65 m (NZOI, 3 v); I71, 29°09.8'S, 168°02.1'E, 57 m (NZOI, 3 v); P36, 29°10.20'S, 168°09.50'E, 76 m (NZOI, 1 v); P38, 29°10.40'S, 167°55.80'E, 64 m (NZOI, 1 v); K819, 29°13.24'S, 177°56.30'W, 100 m (NZOI, 2 v); K820, 29°13.30'S, 177°59.80'W, 95 m (NZOI, 1 fragment); P22, 29°30.90'S, 167°58.80'E, 56 m (NZOI, 1 v); P18, 29°34.60'S, 168°03.00'E, 90 m (NZOI, 4 v). KERMADEC ISLANDS: T233, 29°13.00'S, 178°00.00'W, 100 m (NZOI, 1 v); K820, 29°13.30'S, 177°59.80'W, 95 m (NZOI, 4 v); 29°14.6'S, 177°52.6'W, Meyer I., west-side, 15–30 m (AIM AK.78572, 1 pr); BS573, 29°15'S, 177°50.9'W, between Dayrell and Chanter Is., Herald Is., 31–45 m, R.V. "Acheron" (NMNZ M.227103, 1 juv. pr & 2 v); "Galathea" stn 675, 29°15'S, 177°52'W, off Raoul I., 58–60 m (AMS C81779, 2 v); BS436, 29°18.5'S, 177°54.5'W, SE of D'Arcy Point, Raoul I., 44 m, R.V. "Acheron" (NMNZ M.225783, 3 v); BS572, 29°18.9'S, 177°56.4'W, SE of Smith Bluff, Raoul I., 82–100 m, R.V. "Acheron" (NMNZ M.226585, 4 v); K796, 31°20.8'S, 178°49'W, 70 m, alive (NZOI, 1 pr & 1 v); K797, 31°20.8'S, 178°49.2'W, 55–70 m (NZOI, 6 v).

Distribution: Coral Sea, New Caledonia, Lord Howe Island, Norfolk Island, and Kermadec Islands; 31–183 m, living at 15–55 m.

Remarks: This species is closely similar to *Annachlamys reevei* (Adams in Adams & Reeve, 1850), which ranges from southern Japan to northern Australia, and has recently been found off Somalia (HD colln). Compared with *A. reevei*, *A. iredalei* tends to have more numerous radial ribs (16–18 instead of 16), which are higher and more rounded. Delicate concentric lamellae are developed over the entire shell disc of both species, although they are somewhat interrupted in *A. iredalei*, because of the close-set secondary radial riblets on the costae.

Pecten flabellatus Lamarck, 1819 (northern, western and eastern Australia) differs from *A. iredalei* in having a flatter left valve, slightly larger auricles, less prominent rounded costae, and in lacking secondary radial riblets.

Plate 10. Figures 1–7. *Annachlamys iredalei* (Powell, 1958), Kermadec Islands, 70 m, NZOI. Figs. 1–4 (scale = 5 mm), figs. 5–7 (scale = 1 mm). Fig. 1. Left valve, interior. Fig. 2. Left valve, exterior. Fig. 3. Right valve, exterior. Fig. 4. Right valve, interior. Fig. 5. Left valve, exterior, microsculpture, ventral area. Fig. 6. Right valve, exterior, microsculpture, postero-ventral area. Fig. 7. Right valve, interior, anterior auricle, ctenolium.
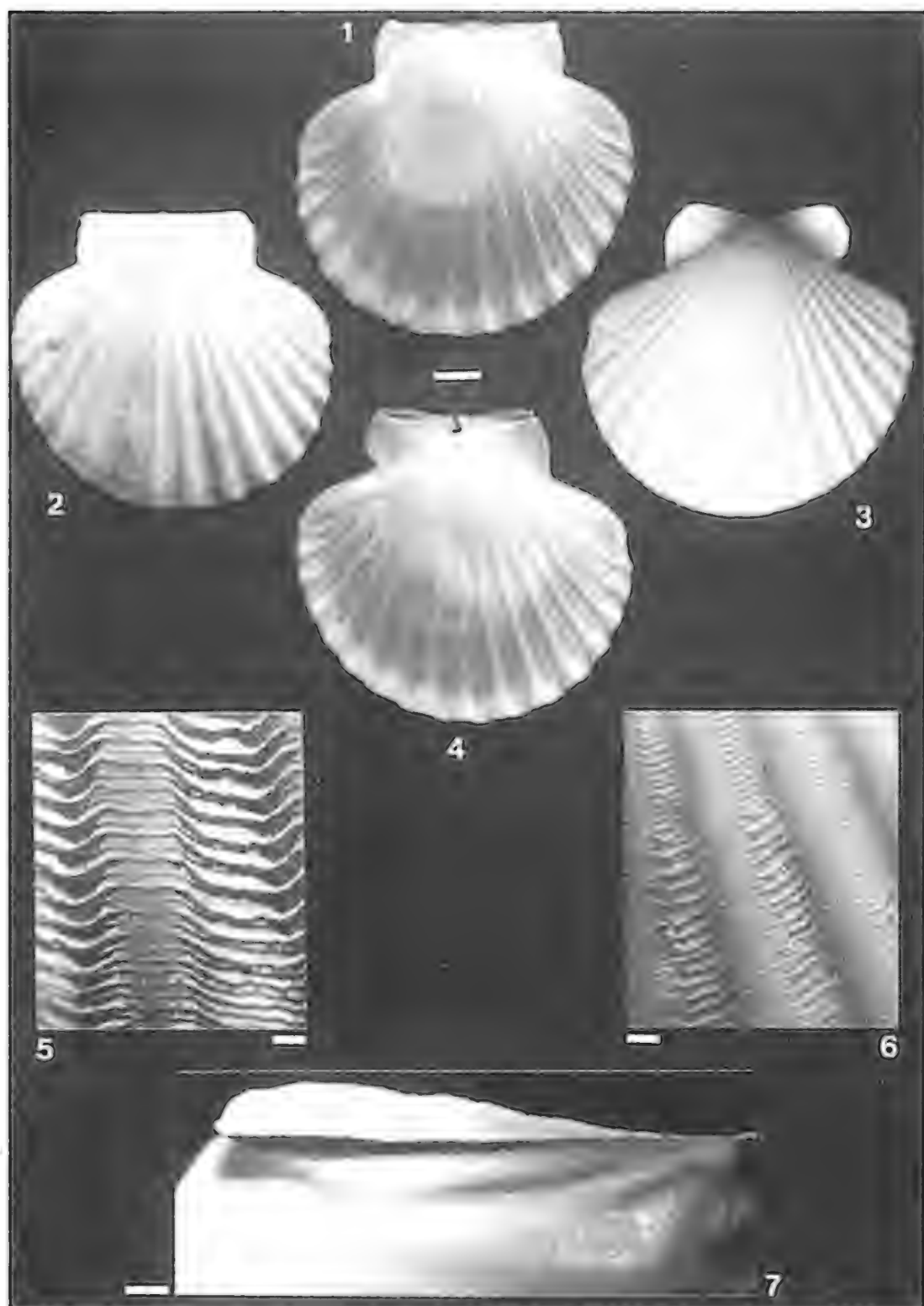
Annachlamys kuhnholtzi (Bernardi, 1860)

Plate 11, figs. 1–7

Pecten kuhnholtzi Bernardi, 1860: 378–379, pl. 13, fig. 1.

Annachlamys leopardus rena Iredale, 1939: 359 (**Syn. nov.**).

Annachlamys kuhnholtzi (Bernardi). Dijkstra, 1986: 19, 21, figs.

Annachlamys flabellata kuhnholtzi (Bernardi). Dijkstra et al., 1990: 9, 10, fig.

Annachlamys flabellata (Lamarck). Lamprell & Whitehead, 1992: pl. 11, fig. 63 (partly not Lamarck, 1819).

Type data: *Pecten kuhnholtzi*: Holotype MNHN, New Caledonia. *Annachlamys leopardus rena*: Holotype AMS C.119783, 23°18'S, 151°42'E, North-West Island, Capricorn Group, Queensland.

Other material examined: LORD HOWE ISLAND: P106, 31°27.7'S, 159°02.6'E, alive, 53 m (NZOI, 1 pr); P112, 31°34.6'S, 159°07.9'E, alive, 50 m (NZOI, 2 pr); H.M.A.S. "Kimbla" stn LH 1, 31°34.9'S, 159°1.3'E, 73 m (AMS C.123973, 9 v); H.M.A.S. "Kimbla" stn LH 4, 31°37.1'S, 159°13'E, 51–55 m (AMS C.123846, 6 v).

Distribution: Coral Sea, New Caledonia, eastern Australia and Lord Howe Island; 8–73 m, living at 10–69 m.

Remarks: *Annachlamys leopardus rena* Iredale, 1939, based on material from Queensland, is indistinguishable from the holotype and other New Caledonian specimens of *A. kuhnholtzi*, and we consider them synonyms. Allopatric populations of *A. flabellata* from Australia will be discussed elsewhere. The present material from Lord Howe Island is similar to the type specimen of *P. kuhnholtzi*.

Subfamily Chlamydinae von Teppner, 1822

Tribe Chlamydini von Teppner, 1822

Genus *Chlamys* Röding, 1798

Chlamys Röding, 1798: 161. Type species (by subsequent designation of Herrmannsen, 1847): *Pecten islandicus* Müller, 1776; Recent, N Atlantic.

Chlamys coruscans coruscans (Hinds, 1845)

Plate 8, figs. 7–10

Pecten coruscans Hinds, 1845: 61–62, pl. 17, fig. 3; Reeve, 1853: sp. no. 149 (not 143), pl. 33, fig. 149; Küster & Kobelt, 1888: 259, pl. 67, fig. 9.

Pecten cuneolus Reeve, 1853: sp. no.131, pl. 29, fig. 131.

? *Pecten schmeltzii* Dunker in Küster & Kobelt, 1888: 272, pl. 71, figs. 5–6.

Pecten sulphureus Dunker in Küster & Kobelt, 1888: 276, pl. 72, figs. 5–6 (not Bosc, 1802, not Lamarck, 1819).

◀ Plate 11. Figures 1–7. *Annachlamys kuhnholtzi* (Bernardi, 1860), Lord Howe Island, 53 m, NZOI. Figs. 1–4 (scale = 10 mm), figs. 5–7 (scale = 1 mm). Fig. 1. Left valve, interior. Fig. 2. Left valve, exterior. Fig. 3. Right valve, exterior. Fig. 4. Right valve, interior. Fig. 5. Left valve, exterior, commarginal microsculpture, postero-ventral area. Fig. 6. idem, antero-ventral area. Fig. 7. Right valve, interior, antero-dorsal area.

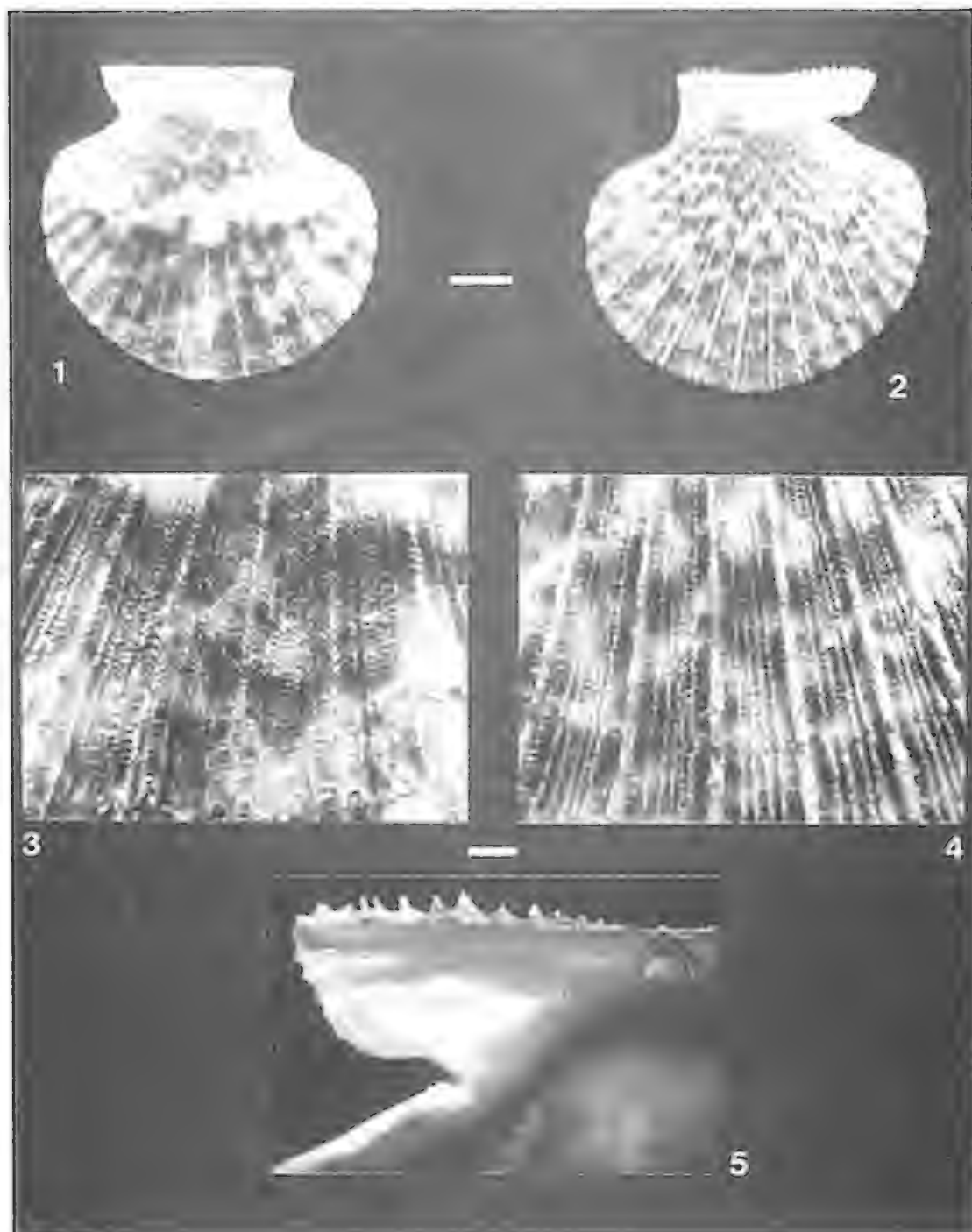Plate 12.   Figures 1–5. *Cryptopecten bullatus* (Dautzenberg & Bavay, 1912), Kermadec Islands, 154 m, NMNZ M.225419. Figs. 1–2 (scale = 5 mm), figs. 3–5 (scale = 1 mm). Fig. 1. Left valve, exterior. Fig. 2. Right valve, exterior. Fig. 3. Left valve, exterior, microsculpture, postero-ventral area. Fig. 4. Right valve, exterior, microsculpture, postero-ventral area. Fig. 5. Right valve, interior, anterior auricle, ctenolium.

Pecten kermadecensis Oliver, 1911: 527 (not E. A. Smith, 1885); 1915: 554.

Chlamys cellularis Oliver, 1915: 554, pl. 12, fig. 46 (**Syn. nov.**).

Pecten eucosmia Turton, 1932: 222, pl. 57, fig. 1549.

Chlamys coruscans (Hinds). Dautzenberg & Bouge, 1933: 426; Waller, 1972: 231–236, pl. 1, figs. 1–19, figs. 2, 12, 14, table 2; Kilburn & Rippey, 1982: 171, pl. 38, fig. 10; Dijkstra, 1984: 9–10, figs.; 1989b: 12, figs.; 1990: 3–5, figs.; Dijkstra et al., 1989: 24; Rombouts, 1991: 10, pl. 23, figs. 7–7b; Lamprell & Whitehead, 1992: text unpag., pl. 8, fig. 47.

Chlamys schmeltzi (Dunker). Kira, 1962: 137, pl. 49, fig. 10.

Bractechlamys schmeltzi (Dunker). Wang, 1983b: 531, 532, 533, 534, figs. 4–7.

Type data: *Pecten coruscans*: Lectotype BMNH 19709 (Waller 1972: 231), Port Anna Maria, Nukuhiva, Marquesas Islands, 13 m. *Pecten cuneolus*: Lectotype BMNH 1969140 (Waller 1972: 231), "Durban, Natal". *Pecten schmeltzii*: 5 ?Syntypes MNHB, "Upola, Samoa and Viti-Inseln". *Pecten sulphureus*: Holotype MNHB, "An den Viti-Inseln". *Pecten eucosmia*: Holotype OUZM Turton No. 1549, Port Alfred, Zululand, South Africa. *Chlamys cellularis*: Holotype (lv) CM M.688, Beach, Sunday [= Raoul] Island, Kermadec Islands.

Other material examined: LORD HOWE ISLAND: Erscott's Hole, 31°33'S, 159°05'E, alive, 3 m (AMS C.157580, 1 pr); Erscott's Hole, 31°33'S, 159°05'E, reef, 8 m (AMS C.300126, 1 v); H.M.A.S. "Kimbla" stn LH 2, 31°38.2'E, 159°3.6'E, 44 m (AMS C.300123, 1 v). NORFOLK ISLAND: AUZ27, 28°53'S, 168°03'E, NE of Norfolk I., 46 m, R.N.Z.F.A. "Tui" (NMNZ M.223538, 1 pr). KERMADEC ISLANDS: Low flat beach, Sunday I. (NMNZ M.214629, 4 v); Raoul I. (NMNZ M.202881, 2 pr); Raoul I. (AMS C.300125, 9 v); Raoul I., north coast (AIM AK.79528, 9 v); 29°14.6'S, 177°52.6'E, west side of Meyer I. (AIM AK.78582, 3 v).

Distribution: Zululand, Natal, Zanzibar, Mauritius, Maldives, Cocos-Keeling Islands, southern Japan, southern China, Philippines, eastern Australia, Mariana Islands, Caroline Islands, Marshall Islands, Gilbert Islands, Fiji Islands, French Polynesia; 0–82 m, living intertidally to 24 m.

Remarks: The type specimen of *C. cellularis* and other specimens from the Kermadec Islands and Norfolk Island are similar in shell morphology to the type specimens of *C. coruscans*. A geographic subspecies, *Chlamys coruscans hawaiensis* Dall, Bartsch & Rehder, 1938 (Waller, 1972: 232) occurs off Hawaii. A closely allied form is *Chlamys pasca* (Dall, 1908) from Easter Island, which could also represent a local population of *C. coruscans*. Waller (1972: 233) has discussed the ecology of this species.

The fossil species from Dayrell Islet (Pleistocene) recorded by Oliver (1911) as *Pecten kermadecensis* E. A. Smith, 1885 is also *P. c. coruscans* (Oliver, 1915; Marshall, 1981).

<div align="center">

Tribe Mimachlamydini Waller, 1993

Genus *Mimachlamys* Iredale, 1929

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Mimachlamys Iredale, 1929: 162. Type species (by original designation): *Pecten asperrimus* Lamarck, 1819; Recent, Australia.

Remarks: Waller (1991: 31; 1993: 200) firmly established the differences between *Chlamys* Röding, 1798 and *Mimachlamys* Iredale, 1939, and placed the latter genus in the tribe *Mimachlamydini*.

<div align="center">

Mimachlamys senatoria (Gmelin, 1791)

Plate 9, figs. 1–4

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Pallium senatoris Chemnitz, 1784: 320, pl. 65, fig. 617 (not binomial).

Pallium porphyreum Chemnitz, 1784: 330, pl. 66, fig. 632 (not binomial).

Ostrea senatoria Gmelin, 1791: 3327 (based on Chemnitz, 1784: 320, pl. 65, fig. 617).

Ostrea porphyrea Gmelin, 1791: 3328 (based on Chemnitz, 1784: 330, pl. 66, fig. 632).

Pecten aurantius Lamarck, 1819: 175.

Pecten florens Lamarck, 1819: 175.

Pecten indicus Deshayes, 1832: 410–411, pl. 3, fig. 5.

Pecten pseudolima Sowerby, 1842: 78, pl. 20, fig. 235; Reeve, 1853: sp. no. 57, pl. 16, figs. 57a–b.

Pecten layardi Reeve, 1853: sp. no. 80, pl. 21, figs. 80a–b.

Pecten fricatus Reeve, 1853: sp. no. 161, pl. 34, fig. 161.

Pecten blandus Reeve, 1853: sp. no. 162, pl. 34, figs. 162a–b.

Pecten raffrayi Jousseaume, 1886: 221–222, fig.

Pecten (Chlamys) senatoria (Gmelin). Dautzenberg & Bavay, 1912: 4–8.

Mimachlamys ellochena Iredale, 1939: 349, pl. 5, fig. 24.

Chlamys (Mimachlamys) asperrimoides Powell, 1958: 70, pl. 11, figs. 3–4, text fig. 3 (**Syn. nov.**).

Chlamys senatoria (Gmelin). Barnard, 1964: 430; Abbott & Dance, 1982: 309, fig.; Dijkstra, 1990a:
    9, 11; Dharma, 1992: 84–85, pl. 20, figs. 3–3a; Oliver, 1992: 74, pl. 13, figs. 1a–b.

Mimachlamys senatoria (Gmelin). Dijkstra et al., 1989: 24; Dijkstra,1990a: 6–8, figs.; 1991: 34–35;
    Lamprell & Whitehead, 1992: text unpag., pl. 10, fig. 56; Dijkstra, 1993: 12–13, figs. 1–5.

Chlamys (Mimachlamys) senatoria (Gmelin). Rombouts, 1991: 30 (partly), pl. 11, figs. 6–6a.

Mimachlamys asperrimoides (Powell). Lamprell & Whitehead, 1992: text unpag., pl. 10, fig. 57.

Type data: *Ostrea senatoria*: Lectotype (here designated) ZMUC BIV–45, "Oceano indico" (Indian
Ocean). An articulated specimen was in the Moltke collection (now ZMUC), and figured in Chemnitz
(1874: pl. 65 fig. 617). *Ostrea porphyrea*: Lectotype (lv)(here designated) ZMUC BIV–46, figured in
Chemnitz (1784: pl. 66 fig. 632); paralectotype (rv) ZMUC BIV–47, "Mari rubro" (Red Sea). Both
valves in Spengler collection (now ZMUC). *Pecten aurantius*: Lectotype (Dijkstra, 1995) MNHN,
"l'Océan indien?". *Pecten florens*: Holotype MHNG 1088/70, "l'Océan indien?". *Pecten indicus*:
Type material not seen (repository unknown). *Pecten pseudolima*: 3 syntypes BMNH 1950.11.14.54–
56, Jacna, Bohol, Philippines. *Pecten layardi*: 6 syntypes BMNH 1994.162, "Ceylon" (Sri Lanka).
Pecten fricatus: Holotype BMNH 1994.161, locality unknown. *Pecten blandus*: 5 syntypes BMNH
1950.11.14.13–17, Australia. *Pecten raffrayi*: Holotype MNHN, Zanzibar. *Mimachlamys ellochena*:
Holotype AMS C.119511, G.B.R. stn XVII, off Shaw Islands, Whitsunday Group, Queensland, 37
m. *Chlamys (Mimachlamys) asperrimoides*: Holotype AIM TM.1235, CS "Recorder", S of Norfolk
Island, from cable, 82–91 m; paratype, ZMUC, "Galathea" stn 674, 29°15'S, 177°57'W, off Raoul
Island, Kermadec Islands, 75–85 m.

Other material examined: LORD HOWE ISLAND: P114, 31°23.9'S, 159°05.4'E, alive, 85–80 m
(NZOI, 1 pr); P106, 31°27.7'S, 159°02.6'E, 53 m (NZOI, 1 v); P104, 31°30.0'S, 159°10.0'E, 75–72
m (NZOI, 2 v); P111, 31°37.6'S, 159°12.4'E, alive, 57 m (NZOI, 1 pr); P82, 31°49.8'S, 159°19.7'E,
78–84 m (NZOI, 1 pr). NORFOLK ISLAND: 1.5 miles SW of Anson Bay, 33–37 m, C.S. "Matai"
(NMNZ M.243283, 4 pr & 1 v); I75, 28°45.0'S, 167°55.2'E, alive, 70 m (NZOI, 8 pr & 6 v); P28,
28°49.8'S, 167°59.6'E, alive, 53 m (NZOI, 4 pr & 3 v); AUZ026, 28°50'S, 168°03'E, NE of Norfolk
I., 55 m, R.N.Z.F.A. "Tui" (NMNZ M.224615, 2 v); AUZ023, 28°51'S, 168°05'E, NE of Norfolk I.,
66 m, R.N.Z.F.A. "Tui" (NMNZ M.223529, 18 v); AUZ027, 28°53'S, 168°03'E, NE of Norfolk I.,
46 m, R.N.Z.F.A. "Tui" (NMNZ M.223538, 1 v); AUZ022, 28°53'S, 168°07'E, NE of Norfolk I.,
95–104 m, R.N.Z.F.A. "Tui" (NMNZ M.223563, 5 v); AUZ028, 28°54'S, 167°59'E, N of Norfolk I.,
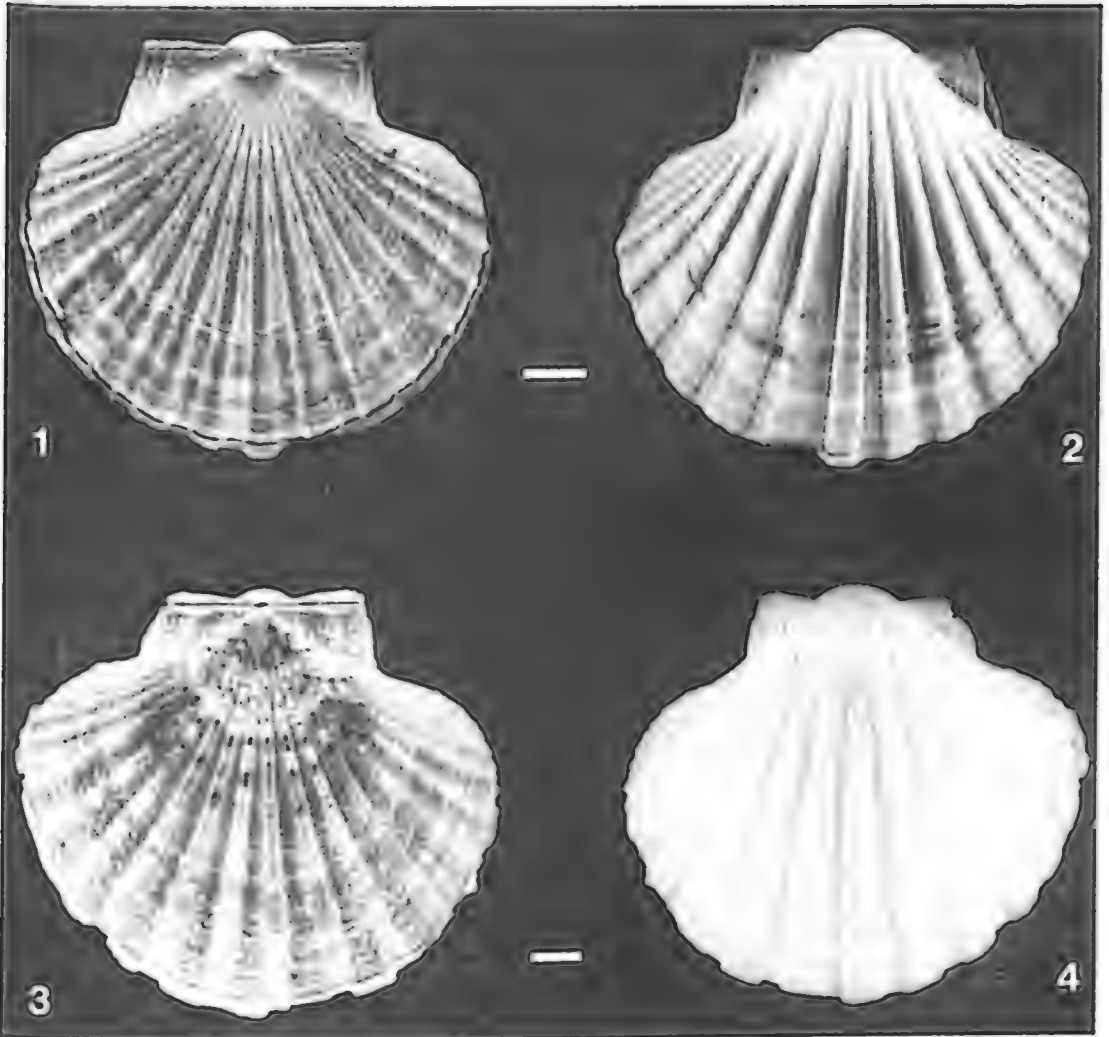
Plate 13. Figures 1–2. *Pecten fumatus* Reeve, 1852, Lord Howe Island, 53 m, NZOI stn P106. Figs. 1–2 (scale = 10 mm). Fig. 1. Left valve, exterior. Fig. 2. Right valve, exterior. Figures 3–4. *Pecten raoulensis* Powell, 1958, Kermadec Islands, 110–121 m, NMNZ M.222134. Figs. 3–4 (scale = 10 mm). Fig. 3. Left valve, exterior. Fig. 4. Right valve, exterior.

33 m, R.N.Z.F.A. "Tui" (NMNZ M.224554, many v); 174, 28°54.9'S, 167°55.5'E, 44 m (NZOI, 17 v); AUZ29, 28°56'S, 167°58'E, N of Norfolk I, 38 m, R.N.Z.F.A. "Tui" (NMNZ M.224926, 28 v); AUZ030, 28°59'S, 167°58'E, N of Norfolk I, 38 m, R.N.Z.F.A. "Tui" (NMNZ M.225103, many v); 173, 29°00.2'S, 168°00.8'E, 51 m (NZOI, > 50 v); 172, 29°04.4'S, 168°01.0'E, 55 m (NZOI, 12 v); 181, 29°06.0'S, 167°56.3'E, alive, 37 m (NZOI, 12 pr & > 50 v); 180, 29°06.8'S, 167°56.7'E, 34 m (NZOI, 1 v); 182, 29°07.7'S, 168°00.3'E, alive, 51 m (NZOI, > 50 pr & > 50 v); 184, 29°07.8'S, 168°09.9'E, alive, 65 m (NZOI, > 100 pr & > 50 v); 171, 29°09.8'S, 168°02.1'E, 57 m (NZOI, > 50 v), P36, 29°10.2'S, 168°09.5'E, 76–80 m (NZOI, 15 v); AUZ36, 29°19'S, 168°07'E, off Norfolk I, 110 m, R.N.Z.F.A. "Tui" (NMNZ M.224931, 44 v); AUZ037, 29°20'S, 168°09'E, E of Norfolk I, 201 m, R.N.Z.F.A. "Tui" (NMNZ M.224719, many v); 190, 29°25.0'S, 168°05.6'E, alive, 71 m (NZOI, 18 pr & > 100 v); P21, 29°31.8'S, 167°59.2'E, alive, 52 m (NZOI, 2 pr & 18 v); P19,

29°33.6'S, 168°01.6'E, 81–80 m (NZOI, 17 v); P18, 29°34.60'S, 168°03.00'E, 90 m (NZOI, 1 v). KERMADEC ISLANDS: K829, 29°13.00'S, 177°52.40'W, 610 m (NZOI, 1 v); T225, 29°13.10'S, 177°53.50'W, 472 m (NZOI, fragment).

Distribution: Throughout the tropical and subtropical Indo-West Pacific; 0–610 m, living at 37–71 m.

Remarks: As indicated by the synonymy, many names are used in literature for this species, and it is often confused with superficially similar species, such as *M. gloriosa* (Reeve, 1853) and *M. nobilis* (Reeve, 1853). Shells are often covered with sponges (Dijkstra, 1993: 12).
   Specimens from the Kermadec Islands and Norfolk Island correspond very well with the type specimen of *M. senatoria*, although they have slightly more strongly lamellate scales on the primary and secondary radial costae, especially when covered by sponges. This phenomenon, however, is frequently observed in other species of *Mimachlamys*, and in *Chlamys* and *Zygochlamys*.

Genus *Talochlamys* Iredale, 1929

Talochlamys Iredale, 1929: 164. Type species (by original designation): *Chlamys famigerator* Iredale, 1925; Recent, off New South Wales, Australia.

Remarks: Species of *Talochlamys* differ from *Mimachlamys* Iredale, 1929 by attaining smaller size, by being more weakly convex, and in having irregularly spaced radial costae, and interstitial concentric lamellae. Moreover, the secondary radial riblets are weaker and less regularly developed, while there are fine grooves on the anterior and posterior margins. In some specimens, however, the sculpture may be interrupted and followed by a sculpture similar to that in *Mimachlamys*. See also Beu (1995: 17).

Talochlamys sp. cf. *pulleineana* (Tate, 1887)

Pecten pulleineanus Tate, 1887: 73, pl. 4, figs. 1a–b.

Chlamys antiaustralis Hedley, 1911: 96 (partly); 1917: M8 (not *Pecten antiaustralis* Tate).

Chlamys famigerator Iredale, 1925: 252–253, pl. 41, figs. 1–2.

Mimachlamys famigerator (Iredale). Cotton & Godfrey, 1938: 100–102, fig. 88; Cotton, 1961: 107–107, fig. 92; Iredale & McMichael, 1962: 11; Lamprell & Whitehead, 1992: text unpag., pl. 9, fig. 53.

Belchlamys atkinos [sic] (Petterd). Cotton, 1961: 101 (not *Pecten aktinos* Petterd).

Camptonectes famigerator (Iredale). Macpherson & Gabriel, 1962: 302, figs. 343, a.

Chlamys (Talochlamys) famigerator Iredale. Rombouts, 1991: 34.

Talochlamys pulleineana (Tate). Beu, 1995: 17.

Type data: *Pecten pulleineanus*: Holotype (rv) SAM D.14171, "South-East coast" (of Australia). *Chlamys famigerator*: Syntypes (1 lv, 1 rv) AMS C.53767, off Green Cape, southern New South Wales, 91–128 m.

Other material examined: NORFOLK RIDGE: BS891 (0637), 32°39.2'S, 167°31.7'E, Wanganella Bank, 133 m, R.V. "Tangaroa" (NMNZ M.243282, 3 v).

Distribution: Norfolk Ridge, New South Wales, Victoria, Tasmania, South Australia and Western Australia; 73–1000 m, living at 128–586 m.

Remarks: Cotton (1961) treated *Talochlamys pulleineanus* as a junior synonym of *Chlamys aktinos*

Table 1. Pectinoidea of Lord Howe Island (LH), Norfolk Island (N) and Kermadec Islands (K).
(o = taken alive; + = taken dead; – = no records)

Species	LH	N	K
1. *Propeamussium alcocki*	–	+	–
2. *P. maorium*	–	+	o
3. *P. rubrotinctum*	–	+	–
4. *P. sibogai*	–	–	+
5. *Parvamussium cristatellum*	–	–	+
6. *P. retiaculum*	–	+	+
7. *P. squalidulum*	–	–	o
8. *P. vesiculatum*	–	o	–
9. *Cyclochlamys lemchei*	–	–	o
10. *Cyclopecten horridus*	–	–	o
11. *C. kapalae*	–	–	o
12. *C. kermadecensis*	–	–	o
13. *Amusium balloti*	–	+	–
14. *Hemipecten forbesianus*	–	+	–
15. *Delectopecten musorstomi*	–	+	–
16. *Chlamys coruscans coruscans*	+	o	o
17. *Mimachlamys senatoria*	o	o	o
18. *Talochlamys* sp. cf. *pulleineanus*	–	+	–
19. *Annachlamys iredalei*	o	o	o
20. *A. kuhnholtzi*	o	–	–
21. *Cryptopecten bullatus*	+	+	o
22. *Cryptopecten nux*	+	–	–
23. *Pecten fumatus*	o	–	–
24. *Pecten raoulensis*	–	–	o

(Petterd, 1886). From examination of type material, however, we conclude that *T. pulleineanus* is a senior synonym of *C. famigerator*, and that *C. aktinos* is a distinct species. *C. aktinos* differs in having shagreen microsculpture instead of radial scratches. The specimens from the Norfolk Ridge closely resemble Australian species of *T. pulleineanus*, but differ in having finer, more widely spaced radial costae, and finer, more closely spaced interstitial concentric lamellae.

Tribus Aequipectinini Nordsieck, 1969

Genus *Cryptopecten* Dall, Bartsch & Rehder, 1938

Cryptopecten Dall, Bartsch & Rehder, 1938: 84, 93. Type species (by original designation): *Cryptopecten alli* Dall, Bartsch & Rehder, 1938 (junior synonym of *Pecten (Chlamys) bullatus* Dautzenberg & Bavay, 1912); Recent, Hawaii Islands.

Corymbichlamys Iredale, 1939: 347, 367. Type species (by original designation): *Chlamys corymbiatus* [sic] Hedley, 1909 (junior synonym of *Pecten nux* Reeve, 1853); Recent, off Hope Islands, Queensland.

Cryptopecten bullatus (Dautzenberg & Bavay, 1912)

Plate 12, figs. 1–5

Pecten (Chlamys) bullatus Dautzenberg & Bavay, 1912: 17–18, pl. 27, figs. 1–2.

Chlamys (Aequipecten) tissotii (Bernardi). Kuroda, 1932: app. 95 (not Bernardi, 1861).

Cryptopecten alli Dall, Bartsch & Rehder, 1938: 93–94, pl. 23, figs. 1–4, 7; Poutiers, 1981: 332; Abbott & Dance, 1982: 308, holotype figured; Dijkstra, 1987: 8, fig.

Chlamys bullatus (Dautzenberg & Bavay). Barnard, 1964: 429–430, fig. 14c.

Cryptopecten tissotii (Bernardi). Habe, 1951: 77; 1964b: 174, pl. 53, fig. 8; Okutani, 1972: 113, fig. 62; Habe, 1977: 84; Koyama et al., 1981: 67 (not Bernardi, 1861).

Cryptopecten complanus Wang, 1983a: 402–403, 405–406, figs. 1.1–7.

Cryptopecten bullatus (Dautzenberg & Bavay). Hayami, 1984: 96–99, pl. 1, figs. 1–6, pl. 2, figs. 1–3, pl. 9, fig. 1, pl. 10, fig. 3, pl. 11, fig. 3; Wagner, 1989: 60–61, figs. 14–16; Dijkstra, 1991: 4, 35–36; 1992: 26–28, figs.; 1995: 51, figs. 115–118.

Chlamys alli (Dall, Bartsch & Rehder). Earle, 1985: 1, 4, 5, figs.

Chlamys (Cryptopecten) bullatus (Dautzenberg & Bavay). Rombouts, 1991: 23–24, pl. 23, fig. 6.

Type data: *Pecten (Chlamys) bullatus*: Holotype ZMA Moll.3.12.006, "Siboga" stn 105, 6°8'N, 121°19'E, Sulu Archipel, 275 m. *Cryptopecten alli*: Holotype USNM 173194, "Albatross" stn 3811, S coast of Oahu, Hawaiian Islands, 435–461 m. *Cryptopecten complanus*: Holotype IOAS M11072, 31°05'N, 128°00'E, East China Sea, 147 m.

Other material examined: LORD HOWE ISLAND: Q67, 29°30.5'S, 159°03.3'E, 350–437 m (NZOI, 1 v). NORFOLK ISLAND: AUZ036, 20°19'S, 168°07'E, off Norfolk I., 110 m, R.N.Z.F.A. "Tui" (NMNZ M.224931, 2 v); AUZ037, 20°20'S, 168°09'E, off Norfolk I., 201 m, R.N.Z.F.A. "Tui" (NMNZ M.224719, 19 v); I94, 29°20.2'S, 168°10.8'E, 308 m (NZOI, 6 v); P16, 29°36.3'S, 168°05.0'E, 310 m (NZOI, 1 v); P48, 28°42.8'S, 167°54.6'E, 279–186 m (NZOI, 2 v). KERMADEC ISLANDS: AUZ113, off Curtis I., 302 m, R.N.Z.F.A. "Tui" (NMNZ M.224642, 1 v); BS307, between Bell's Flat and Hutchison Bluff, Raoul I., alive, 110–146 m, R.V. "Acheron" (NMNZ M.222112, 1 pr); BS437, 29°11.9'S, 177°56.2'W, NW of Fleetwood Bluff, Raoul I., alive, 154 m, R.V. "Acheron" (NMNZ M.225419, 1 pr & 2 v); BS434, 29°12.7'S, 177°56.1'W, NW of Fleetwood Bluff, Raoul I., alive, 135 m, R.V. "Acheron" (NMNZ M.225425, 1 pr & 11 v); K816, 29°13.04'S, 177°55.5'W, 22–80 m (NZOI, 1 v); BS438, 29°14.7'S, 177°49.4'W, SE of Nugent I., Raoul I., alive, 146–165 m, R.V. "Acheron" (NMNZ M.225723, 2 pr & 24 v); BS570, 29°14.73'S, 177°50.34'W, E of Dayrell I., Herald Is., alive, 135–146 m, R.V. "Acheron" (NMNZ M.226627, 5 pr & 7 v); BS441, 29°15.5'S, 177°50'W, E of Chanter Is., Raoul I., 366–402 m, R.V. "Acheron" (NMNZ M.225506, 6 v); K803, 29°16.0'S, 177°50.3'W, alive, 140 m (NZOI, 1 pr); BS572, 29°18.9'S, 177°56.4'W, SE of Smith Bluff, Raoul I., alive, 82–100 m, R.V. "Acheron" (NMNZ M.27159, 2 pr & 3 v); K826, 28°48'S, 177°48'W, 142–160 m (NZOI, 1 v); K840, 30°17.6'S, 178°25.3'W, 398–412 m (NZOI, 1 v); K842, 30°10.2'S, 178°35.9'W, alive, 325–370 m (NZOI, 1 pr & 1 v); K856, 30°33.5'S, 178°31.1'W, 125–130 m (NZOI, 14 v); K875, 30°33.8'S, 178°30.6'W, 165–180 m (NZOI, 9 v).

Distribution: SW Indian Ocean, SE Africa, central and southern Japan, East China Sea, Philippines, Indonesia, E Australia, New Caledonia, Lord Howe Island, Norfolk Island, Kermadec Islands, Hawaiian Islands; 64–571 m, living at 82–461 m.

Remarks: Several Japanese authors have misidentified specimens of *C. bullatus* as *P. tissotii* Bernardi, 1858, but the type specimen of the latter (MNHN) is a juvenile *Aequipecten flabellum* (Gmelin, 1791) described from an unknown locality (off western Africa, det. Dijkstra – see also Hayami, 1984: 98). Poutiers (1981) identified a single right valve from northern Lubang, Philippines as *Cryptopecten alli*, but Hayami (1984) showed that *C. alli* and *C. bullatus* are identical in shell morphology and synonymized them. *C. complanus* Wang, 1983, based on material from East China Sea, is weakly differentiated from *C. bullatus* and is perhaps merely a local population.
Specimens from the Kermadec Islands and Norfolk Island are slightly more convex than the type

Table 2. Pectinoidea of Lord Howe Island, Norfolk Island and the Kermadec Islands in common to other regions. (I = Indonesia; NA = Northern Australia; EA = Eastern Australia; SEA = Southeastern Australia; SWA = Southwestern Australia; CS = Coral Sea; NC = New Caledonia; L = Loyalty Islands; V = Vanuatu; LH = Lord Howe Island; N = Norfolk Island; K = Kermadec Islands; NZ = New Zealand)

Species	I	NA	EA	SEA	SWA	CS	NC	L	V	LH	N	K	NZ
Propeamussium alcocki	x					x	x	x			x		
P. maorium											x	x	x
P. rubrotinctum	x						x	x			x		
P. sibogai	x	x				x	x	x				x	
Parvamussium cristatellum	x											x	
P. retiaculum							x				x	x	
P. squalidulum						x		x	x			x	
P. vesiculatum							x	x			x		
Cyclochlamys lemchei												x	
Cyclopecten horridus							x	x				x	
C. kapalae				x								x	
C. kermadecensis												x	
Amusium balloti	x			x	x	x	x				x		
Hemipecten forbesianus	x		x	x	x	x	x				x		
Delectopecten musorstomi	x						x				x		
Chlamys coruscans	x		x			x	x	x	x	x	x	x	
Mimachlamys senatoria	x	x	x			x	x			x	x	x	
Talochlamys sp.				x	x						x		
Annachlamys iredalei						x	x			x	x	x	
A. kuhnholtzi			x			x	x			x			
Cryptopecten bullatus	x					x	x	x	x	x	x	x	
C. nux	x		x			x	x			x			
Pecten fumatus			x	x	x					x			
P. raoulensis												x	
	11	2	6	5	4	11	15	8	3	7	13	14	1

specimen of *C. bullatus*, but intermediate forms are common. The sculpture in this species is rather variable, the interstitial concentric lamellae ranging from strong to very weak, though there is complete integradiation between extremes both within and between populations.

Cryptopecten nux (Reeve, 1853)

Pecten coruscans (not Hinds). Reeve, 1853: sp. 143, pl. 32, fig. 143.

Pecten nux Reeve, 1853: note under sp. 149.

Pecten hastingsii Melvill, 1888: 279, pl. 2, fig. 7.

Pecten guendolenae Melvill, 1888: 279, pl. 2, fig. 6.

Chlamys smithi G.B. Sowerby III, 1908: 18, pl. 1, figs. 6–7.

Chlamys corymbiatus Hedley, 1909: 423, pl. 36, figs. 1–4.

Corymbichlamys corymbiatus (Hedley). Iredale, 1939: 368.

Cryptopecten nux (Reeve). Habe, 1951: 77; 1961: 118, pl. 53, fig. 9; 1964b: 174, pl. 53, fig. 9; Dijkstra, 1991: 36–37; Lamprell & Whitehead, 1992: pl. 11, fig. 66.

Cryptopecten nux nux (Reeve). Hayami, 1984: 100–103, pl. 2 fig. 4, pl. 3, figs. 1, 2, pl. 9 figs. 2–5, pl. 12, figs. 1, 2.

Cryptopecten bernardi corymbiatus (Hedley). Dijkstra, 1988: 7–8, figs..

Cryptopecten bernardi nux (Reeve). Dijkstra et al., 1990: 9, 10, figs..

Chlamys (Cryptopecten) bernardi (Philippi). Rombouts, 1991: 23, pl. 23, figs. 3, 3a (not Philippi, 1851).

Type data: *Pecten nux*: Lectotype (designated by Wagner, 1989) BMNH 1950.11.14.52 and 2 paralectotypes (BMNH 1950.11.14.50–51), Panglao, Bohol, Philippines (designated by Wagner, 1989). *Pecten hastingsii*: Holotype NMW 1955.158.10, Japan. *Pecten guendolenae*: Holotype NMW 1955.158.02, Mauritius. *Chlamys smithi*: Holotype BMNH 1908.5.30.63, Mauritius. *Chlamys corymbiatus*: 2 syntypes AMS C.27532, Hope Islands, northern Queensland, 9–18 m.

Other material examined: LORD HOWE ISLAND: H.M.A.S. "Kimbla" stn LH 1, 31°34.9'S, 159°0.3'E, 73 m (AMS C.300121, 2 v); H.M.A.S. "Kimbla" stn LH 2, 31°38.2'S, 159°3.6'E, 44 m (AMS C.300122, 2 v).

Distribution: Red Sea, Oman, Kenya, Seychelles, Mozambique, Malagasy, Mauritius, eastern South Africa, Andaman Islands, Japan, Taiwan, Philippines, Indonesia, eastern and northern Australia, Micronesia, Melanesia, Polynesia; 9–918 m, living at 30–240 m.

Remarks: Hayami (1984) discussed the natural history and evolution of *Cryptopecten*. Wagner (1989) resurrected *C. guendolenae* from synonymy under *C. nux*, and treated *C. bernardi* from French Polynesia as another distinct species.

Discussion

In a biogeographic analysis of the Mollusca of the Kermadec Islands, Oliver (1915) recorded 34% as endemic (89 species). In a subsequent analysis Dell (1958) also found 34% (85 species) endemism. Fourteen pectinoidean species are now known from that area, of which 3 are endemic (*Chlamydella lemchei, Cyclopecten kermadecensis* and *Pecten raoulensis*)(21%). Ten species were taken alive and 4 were represented by shells only.

Thirteen species are here recorded from Norfolk Island (4 live, 9 dead; none endemic) and 7 species from Lord Howe Island (5 live, 2 dead; none endemic).

Of the 23 pectinoidean species now known from the these island groups, most are closely related to Indo-Pacific species (14 species, 59%), several to the Australian region (6 species, 26%) and one species to New Zealand (4%).

The pectinoidean composition of the Kermadec Islands, Norfolk Island and Lord Howe Island is:

	Kermadecs	Norfolk	Lord Howe
total	14 spp	13 spp	7 spp
endemic	3 (21%)	–	–
Indo-Pacific	8 (57%)	9 (69%)	4 (57%)
Australia	2 (14%)	3 (23%)	3 (43%)
New Zealand	1 (7%)	1 (8%)	–

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Book review

Seashells of Eastern Arabia by Donald T. Bosch, S. Peter Dance, Robert G. Moolenbeek, and P. Graham Oliver. 1995. Motivate Publishing, Dubai, Abu Dhabi and London, 296 pages, US $ 75 (discounts available for several copies). Available from: Motivate Publishing, London House, 19 Old Court Place, Kensington High Street, London W8 4PL, United Kingdom or Motivate Publishing, PO Box 2331, Dubai, United Arab Emirates.

Rarely does a new shell book make such a stunning impression as this one. Two aspects make it simply **magnificent;** the excellent colour photographs throughout by Neil Fletcher, and the great scientific value of the content. *"Seashells of Eastern Arabia"* provides a wholly new survey within two covers of a previously little-known fauna.

The large format (a little larger than A4) and, in many cases, enlarged photographs of even quite large shells, combined with SEM micrographs or reproductions of original drawings of a wide selection of micromolluscs, and a very valuable new account of **all** the bivalves (even tiny ones) by Graham Oliver, all contribute to make this book essential for both the professional malacologist and the well informed "amateur".

Fittingly, the book is dedicated to the late Kathie Smythe, who so enthusiastically tackled this poorly known fauna. The introduction contains a typically thorough Peter Dance history of the study of the fauna, but it is astonishingly brief – little separates F.W. Townsend, J.C. Melvill and H.E.J. Biggs late last century and early in this one from the recent major contributions by Kathie Smythe, M.D. Gallagher and the authors of this book. It is followed by a helpful ecological review, with excellent colour photos, and a list of Arabic place names.

Then follows the species descriptions, associated much more closely with the illustrations than most such books manage. This main section occupies over 250 pages, and describes 1273 species (864 gastropods, 375 bivalves, 14 chitons, 12 scaphopods, and 4 "shelled" cephalopods). While there clearly is a wealth of micromolluscs not covered here (many no doubt still to be discovered), examples are given of all the major groups, and it appears to me that this book provides a 'fuller coverage of the fauna than almost all other shell books, other than those on the really well described faunas (best exemplified, perhaps, by Tucker Abbott's "American Seashells"). It is pleasing to see all of the shelled heterostrophs (including opisthobranchs and marine pulmonates) included, although there is clearly a remaining opportunity for a popular work on the nudibranchs.

Excellent introductions to morphological terms, a good bibliography, a glossary and a detailed index all contribute to the usefulness and overall high standard of scholarship of this book. Boxes scattered throughout the main text provide interesting sidelights on the history or other significance of particular species or specimens – most notably the two original Melvill and Standen specimens of *Conus clytospira* (now known as *C. milneedwardsi*). Surprising range data can be discovered in here for even quite common, widespread species. Who knew, until now, that *Cymatium parthenopeum* is common in eastern Arabia? Although this superdisperser is widespread in the Mediterranean and in the temperate and tropical Atlantic, it is a warm-temperate "fringe species" in the Pacific, avoiding the central tropics (perhaps out-competed by *C. pileare*?– but **both** occur in eastern Arabia).

As always there are a few points for nitpickers to pounce on. The only one obvious to me is the question of where to put *Colubraria* – Phil Maxwell and I (1987) located it in the Buccinidae, and *"Colubraria" antiquata* in the plesiotritonine genus *Tritonoharpa* (the species is evidently not *T. antiquata*, either, but there are probably many unnamed species in this genus). Many readers will also have differences of opinion with the authors about some of the genera and subgenera used in some groups. But these minor points do not in the least detract from a brilliant work, with the highest quality printing. The previously unknown bivalve fauna is a particular eye-opener, comparable to Graham Oliver's earlier "Bivalved Seashells of the Red Sea" (1992; Hemmen, Wiebaden) in its impact on our knowledge of these molluscan "orphans". However, I am sad to see that (as usual) the enormous "family" Turridae is under-represented with only 26 species.

Popularisation of this group is needed, so that in the long run the awful problems in its classification can be resolved. This book missed an important opportunity here.

The occasional taxonomic revelation that can come to light from a wide reading of faunal surveys such as this one is shown by *Nuculana bellula* (A. Adams, 1856)(p. 204, fig. 900). This name is in current use in New Zealand for the abundant Pliocene to living *Saccella* species of shallow shelf faunas. The New Zealand shell is similar to the one figured by Oliver (see Powell, 1979, p. 359, fig. 85.1) but obviously has coarser sculpture and a significantly shorter anterior end. Usage of this name has followed uncritically from Suter (1913, p. 835–6) who pointed out that Martens (1873, p. 49) had identified the New Zealand species as *Leda concinna* A. Adams, 1856; and yet Suter continued to use *L. bellula*, despite quoting a letter from E.A. Smith pointing out precisely those differences that are obvious from Oliver's illustration. Clearly, the name *L. concinna* needs investigation as a more appropriate one for the New Zealand species. How many more misidentifications of this sort await recognition? The publication of more and better faunal surveys, similar to the present one, will help world malacology become stabilised.

There has probably never before been a book on marine molluscs that so immediately provides easy access to such a previously unknown fauna. The team is to be congratulated on a brilliant job. I cannot recommend this book highly enough for the libraries of all serious students of Mollusca.

Alan Beu

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Shepherd, S. A. and Cannon, J. 1988. Studies on southern Australian abalone (genus *Haliotis*). X. Food and feeding of juveniles. Journal of the Malacological Society of Australia 9: 21-26.

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Short, J. W. and Potter, D. G. 1987. Shells of Queensland and the Great Barrier Reef. Marine Gastropods. Golden Press, Drummoyne, NSW.

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Contents